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Interaction With Plants

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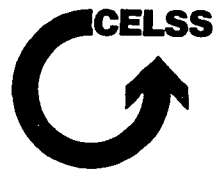
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Literature Review of Human Microbes'
Interaction With Plants

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LITERATURE REVIEW OF HUMAN CARRIED MICROBES'

INTERACTION WITH PLANTS

(NASA (Ames) purchase order A77042 B(ACM), 8/13/80)

ABSTRACT

An analysis of the available literature suggests that human-carried microorganisms, which cannot practically be excluded (at this time) from human supporting agricultural systems of extra-terrestrial stations, may be an important problem. This is because these microorganisms may have several kinds of deleterious effects; some of these, especially those which might damage the plants on which the people depend for oxygen and food, could be extremely serious. It appears that this potential problem can be avoided by the inclusion of carefully screened or constructed, but more or less normal, phylloplane and rhizosphere microbial communities.

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Introduction

This review considers the literature through most of 1980. All of the literature central to the topic of the possible effects of human-carried microbiota on plants (which could be found) is reviewed here. In addition a number of papers from other important closely related areas are considered because the problem clearly is one which will require broad ecological understanding and approach for its resolution, and because this problem will of necessity be only one of many which must be solved as a group if human supporting ecological systems are to function effectively in extraterrestrial situations.

The plan of approach is first to briefly discuss some of the limitations of our knowledge (though we do know much) of microorganisms, with special reference to their systematics, physiology, and ecology. Plant defense mechanisms and plant pathogen attack mechanisms are then briefly discussed. Then the normal microbiota which is associated with plants is examined and the various functions which it serves are elaborated on somewhat. Direct information on microorganisms which are both human and plant pathogens is then given, and finally, possible problems arising from microbial evolution are suggested.

In the discussions below, it has been necessary to restrict the detail of coverage of some of the subjects which are not completely central to the thrust of this paper. The

literature is so large in some of these non-central areas that a complete review would tend to obscure the more important main points and analyses of the paper. Nevertheless, in each of these somewhat peripheral topics, a few of the papers have been considered in order to give at least some detail in support of the generalizations and conclusions which are presented (and to provide entree into the current literature).

The normal microbial biota of human beings.

Savage (1977) makes the dramatic point that of all of the cells which each adult human carries around, only about 1/10th are his own human cells. The other 9/10ths are bacterial, fungal, protozoan, and other kinds of species' cells (which he transports and supports). It would appear that there are well over a hundred species of usually non-pathogenic species in the indigenous microbial flora of normal human adults. Within or on us, each microbial species usually is considerably restricted in its distribution. The human-caused environmental characteristics of the various body areas, and the competitive and antagonistic interactions between various of the microbial species are responsible for these restricted distributions. There is a unique microbial community which is typical of each of our major kinds of regions -- for example on our skin, in our respiratory system, in our gastro-intestinal tract, and so on. Not only is there only a limited overlap with respect to species which are found in each of these general body regions (and especially with

respect to the dominant species), but within each of these regions, there may be considerable limitation to the distribution of many of the species. The papers in Skinner and Carr (1974) provide considerable more detail and an entree into the literature.

Wilson (1974) points up one of the aspects of the activities of our microbiota when he says: "The part played by the normal flora (of humans) in preventing the access of pathogenic bacteria to the tissues is of interest...". The following are a few samples which typify a large literature and which elaborate a little on some of the effects of some of the interactions which may occur between the species which may be found in the various regions of the mammalian body: In the animal models for the human condition, in which some individuals have been "deprived" of their normal microbiota by being aseptically removed from their mothers by cesarean section and by maintenance in germ-proof chambers, inoculation with one to a few of the many species normal to the animal (or to humans) is frequently followed by the establishment of that species' population over a much greater region of the body than occurs in animals which have their normal microbiota. For example, Savage (1978) reports on the yeast, Torulopsis pintolopesii, which is restricted to only the glandular epithelium of the stomach in mice and rats which have their usual microflora: in otherwise microbe free animals, this yeast is able to establish and maintain itself throughout the entire gut (on the epithelium). Even in

originally germfree animals which have been "given back" a number of their normal microbial species the greatly simplified "community" may not be able to limit the yeast to its "proper" location (although the yeast distribution may be considerably reduced from what it was in the otherwise germfree animals. Related results were reported by Pope et al (1979) who found that the sometimes pathogenic yeast Candida albicans would establish persistent infections in the intestines of baby mice, but would not do so when inoculated (in the same way) into adult mice which carried a normal gut flora.

Interactions similar to those which affect the yeast distributions clearly are important to the protection of not only mammals but also other animals and plants from the pathogens which attack them. For example, a number of years ago, Freter (1956) reported that the indigenous gut microbiota of mice and guinea pigs was important in protecting them from attack by Shigella and Vibrio. More recently, Iwanaga et al (1979) observed that Escherichia coli was able to suppress the growth of Vibrio cholerae (which causes mouse cholera) in vitro, although two other bacteria (Staphylococcus aureus and an Enterococcus) did not. Zachar and Savage (1979) found that a smooth colony strain of Listeria monocytogenes which was not able to invade the gut of mice which had a normal flora, could not do so in "specific-pathogen-free" mice, but could invade the gastro-intestinal tracts of mice which were germfree or which contained only Bacteroides and Clostridium populations.

In addition, Roach and Tannock (1979) discovered that gnotobiotic mice (strain BALB/c) were at least partially protected from Salmonella typhimurium by the presence of Lactobacillus, Bacteroides and two species of Clostridium. It is clear, however, that a normal microflora may not protect the bearer from a pathogen - - and the work of Itoh, Ueda, and Fujiwara (1980) illustrates some of the variation on this theme. Two different strains of germfree mice were challenged with inoculation by a pathogenic strain of Escherichia coli, in one strain (IRC) only part of the gut epithelium was ulcerated (in part of the caecum), although in the other mouse strain (CF 1), lesions were spread through much more of the gut. Both strains of mice contained large E. coli populations in their intestines. When the two strains of mice were allowed contact with mice which had normal lab communities of gut microorganisms, and then inoculated with this virulent strain of E. coli, the IRC animals survived and had no lesions on their gut epithelia, while the CF 1 animals died within 2 weeks (and had severe lesions of the epithelium of their gastro-intestinal tract).

A list of some of the mechanisms by which the normal biota of the gut protects animals from attack by pathogens was provided by Roach and Tannock (1979): 1. The growth of the pathogen population is controlled by the same mechanisms which operate within the gut biota itself to keep its own species in check and localized, 2. The indigenous population protects antibodies which have been produced by the host from

destruction by the digestive enzymes of the host, and 3. The normal gut population "primes" the host immunological defense mechanisms so that pathogen individuals are attacked more quickly after their arrival than otherwise would be possible.

Many factors influence both qualitative and quantitative aspects of the microbial communities which we carry with us. These include the individual's age, health, sex, and physiological state, his diet, the nature of the populations which are common in the environment and which gain entrance to us in large numbers (and can survive, at least for a while, after arrival) -- the intestinal difficulties which people frequently have when they go to a different part of the world is evidence of the importance of this -- and many other factors. One of the more recent discoveries is that the emotional state of a mammal may have significant effect on the structure of the intestinal flora at least in mice (Tannock and Savage, 1974) and men (Holdeman, Good, and Moore, 1976).

A number of other processes which are important to our physiology and health are mediated by our microbiota, and this frequently occurs through the operation of mechanisms which are not understood. For example, the presence or absence of the gut microbiota may have important influence on the kinds and/or amounts of enzymes which are secreted into the gut. Kawai (1980) has observed that, at least in rats, the level of beta-glucuronidase and acid phosphatase in the lysosomes of the ileum mucosa were significantly higher in germfree animals than in those with a normal flora. He suggests that in

general, the presence or absence of the microbiota of the gut has influence on a number of the enzymes which are active in the processes of transport, glycolysis, and digestion of food.

Another effect of the microbial community on the function of the gut is in its stimulation of the rate of the motility of the small intestine. In the germfree animal, or in those individuals which have considerably reduced species numbers in their communities, the motility of the small intestine is reduced, and therefore the rate at which the contents are pushed through it is lower (Roach and Tannock, 1979).

In addition, there are gasses, particularly carbon dioxide, with lesser amounts of methane and hydrogen which are produced during the fermentation which occurs in the gut (Brock and Brock, 1978) - - the importance of these to the health of the person is not known, but this, as well as the possible complications which these gasses might pose for a small, closed, human-containing system should not go without attention.

On theoretical grounds, and as a result of much experimental work, it is known that in any isolated set of biological communities there will be a sharing of species if there is enough movement of members of the communities between the isolated areas (MacArthur and Wilson, 1967). If the environments occupied by the isolated communities are sufficiently similar, one would expect that there would be a reduction of the total number of different species with time.

This is because some of the species which originally were living in only some of the communities would be there only because some of their more effective competitors and/or predators would, by chance not be present. With adequate time for dispersal (and especially with the close contact that an extra-terrestrial station likely would impose), all the efficient predators and competitors contained within any of the people's original microbial communities would have opportunity to be dispersed to and to colonize all of the people. In addition, any of the microbial species which engendered a sufficiently effective immune reaction in the host, as long as it was a good enough disperser and colonizer to reach all of the potential hosts in a reasonably short time (and as long as these processes along with the time required for incubation in the host and development of resultant immunity are short enough), would soon disappear from all of the populations. This phenomenon occurs commonly in isolated groups of people (and is related to the fact that after extended isolation, people who return to mix with larger populations frequently all have a rash of colds, and so on). These are consistent with the observations of Tashpulatov and Guseva (1979) that the cosmonauts of Salyut-3 experienced a decline in their natural levels of resistance to disease.

Because it is premature at this time to choose the kinds of agricultural systems which might be used, and it is possible that there will be advantages to the use of natural and/or artificial soils, a short comment on some of the

possible effects of the soil on microbial populations will be given. Soils provide sites for the maintenance of many microbial populations, but populations of the bacteria commonly found in the gastro-intestinal tract of people usually decline relatively rapidly in them. Some of this is because many of the microbes act much like colloids which are charged and which therefore can be rapidly adsorbed onto the surfaces of clays and other materials in the soil (Marshall, 1975 and 1979, Cooper and Morgan, 1979).

As one would expect, numbers of the different species decline at different rates, and the nature of the soil affects the rate of each species' decline. For example, Klein and Casida (1970) concluded that the relatively rapid diminution of species population numbers of Escherichia coli in soil was the result of the relatively high requirements which that species has for concentrated organic nutrients. Papavassiliou and Leonardopoulos (1978) observed the decrease of E. coli populations at rates of about an order of magnitude a month in sterile soils; Enterobacter and Citrobacter had populations which fell more slowly, and the numbers of 3 species of Salmonella (but not of S. typhi) decreased slightly more slowly still. The most rapid declines among the species studied were those of Proteus and Shigella (which plummeted at 5 to 10 orders per month). Papavassiliou and Leonardopoulos agreed that a major factor in the decline of these enteric species of humans was the generally low level of organic matter (available to these bacteria) in the soils.

Two enteric viruses (a poliovirus type 1 and a reovirus type 3) adsorb to clay very rapidly (nearly to completion in 15 minutes), though less rapidly to sand or to soil organic materials. In sterile soils it took 95 and 123 days for the activity of the two viruses to decline by 99%, while in non-sterile soils, it took only 42 and 35 days respectively. This is a clear indication of the importance of the presence of a microbial flora in a soil to the rate at which viruses become inactivated (Sobsey et al, 1980).

One additional aspect of the human microbial problem is that there is considerable and rapid exchange between bacteria of genetic elements, by plasmid transfer and other mechanisms. The result of this is that there is a potential for rapid development of characteristics which are new to a bacterial population. A few interesting examples will be given which, even if they seem unlikely to be important in themselves, suggest implications which might be of greater moment. Fraizer and Zimmerman (1980), for example, found that a plasmid-containing population of Streptococcus faecalis zymogens was more resistant to the lethal effects of ultraviolet light than was a population without the plasmid. Plasmid containing bacteria had slower growth rates than those without; in addition the plasmid containing individuals were immune to a bacteriophage (SLF) which attacked those without the plasmid, and those with plasmids also could produce a hemolysin which the others could not. There are a number of conditions, therefore, under which the plasmid-bearing

population would be the most successful in spite of its less rapid growth rate.

Plasmids carrying resistance to antibiotics also rapidly and easily enter bacterial populations, and in the presence of the antibiotics can result in the development of antibiotic resistant bacterial populations. Petrocheilou, Richmond, and Bennett (1979) report on an interesting case in which the non-treated husband of a woman who was given a course of antibiotics developed and maintained a population of E. coli which was resistant to the antibiotic his wife was taking. Also, in another study of the transmission of antibiotic resistance from one bacterium to another by plasmids, Eylan and Cohen (1979) confirmed what others had observed before, that babies frequently have bacteria with many more R (resistance) factors (which are plasmid-carried) than do adults, even when neither the babies nor the adults is getting or has taken the antibiotics to which the resistance applies. The infants had E. coli with high levels of multiple resistance (frequently to 5 different antibiotics), and in what may have been their first infection with E. coli, did not show the development of repression (a mechanism of prevention of inter-bacterial transfer of the R factors) which characterized the adults.

Our limitations of knowledge:

Difficulties of microbial systematics

There are great difficulties in the identification of the microorganisms. Most work has been done on the pathogenic species and on some other species which are especially easy to obtain and culture. The standard work in the field of bacterial identification (Bergey's Manual, Buchanan and Gibbons (eds.), 8th ed., 1974) has undergone great revision from what it was as the 7th edition (of 1957), and the chairman of the editors of the next forthcoming edition, J. G. Holt, is telling his classes that that new edition will show even more of a break with the previous edition than did the 8th. This is indicative of the ferment in the field which is caused by our great level of ignorance about the systematics of the bacteria. In the 8th edition (unlike what one found in earlier editions) there is considerable admission of ignorance and warning of the reader to be careful (see especially the preface and the addenda to the various groups). Billing (1976) also emphasizes our ignorance of this subject and points out, among other things, that the ready movement of plasmids carrying genes which permit or prohibit a variety of physiological activities on the part of the recipient makes identification via the use of physiological characteristics additionally difficult. She gives an example in which the ability to ferment lactose, which Salmonella typhi "normally" does not have, may be provided by plasmid transfer to the bacterial population. Screening procedures of this S. typhi which use ability to ferment lactose as one of the tests may therefore be used to reach the conclusion that the organism in question is something else; the error thus made could be

especially serious because S. typhi causes typhoid fever, a serious disease in humans.

In addition to the above fundamental kinds of difficulties, there is also a great deal of work, skill, knowledge, and experience which is required for microbe identification.

Microbial biochemical capabilities

The variety of chemical transformations in which many of the microbial species can take part is great (see for example, Bergey's Manual), but it is clear that there are still many and frequently large gaps in our knowledge of these. For example, which of the microbial species have which of the various capacities? There is indeed much which is known, but it is obvious (as is clear from the previous discussion) that there is still much unknown about microbial capabilities with respect to: the nutritional substrates (and combinations thereof) which may be used, the metabolites which are produced and how this production is modified by different environmental conditions under which the microbial species population is living, the particular and perhaps peculiar kinds of molecules (such as antibiotics) which the population can produce, and the affects of environmental conditions on both qualitative and quantitative aspects of that production, and so on.

Microbial ecology

Not only do we have the limitations on our understanding of the ecological aspects of microorganisms discussed in the last section, but, for most species there is an even greater lack of our knowledge concerning what might be considered the normal environments of and (remainder of) ecology of the various already named species of microorganisms. These points will not be dwelt on any more here because aspects of them will be discussed later in considerable detail.

Root support/medium

It is as yet not possible to make decisions concerning the best root medium to be used for each of the various plant species (which have not yet been chosen). The choice may depend in part on which (if any) other functions may be required of the plant substrate. If some nutrient cycling is to be carried out on or in the plant root medium, for example, the most desirable characteristics of that medium could be in part determined by the needs of this process. In any event, some of the considerations (medium characteristics) which must be taken into account, in addition to nutrient provision are:

- a. buffering capacity (pH, nutrient and toxic ions, etc.)
- b. water holding capacity
- c. effect of medium on root structure, strength, and growth - - and therefore on yield of desirable plant product(s)
- d. plant support requirements to be met by the substrate
- e. (as mentioned above) the degree to which in-medium

mineralization may be possible and desirable

- f. properties affecting microbial species populations
- g. and so on.

Bohm (1979) emphasised the importance of the nature of the root medium to the plant and its activities by commenting that the differences in cell and gross structure of roots grown in liquid culture and soil are so great that it is difficult to compare results of experiments concerning root growth when the two contrasting culture conditions are used. MacKey (1973) pointed out that the roots of green plants in soils generally are relatively few, fine, and deeply penetrating, on the other hand, in water culture, they tend to be stout, little branched, and short (at least in wheat). He measured the effects of various kinds of media on gross root structure and reports that in well irrigated sand and perlite, conditions (and root length) were most like those of water culture, in polytherm the response is intermediate, while greatest root length occurred in vermiculite (and soil). On the other hand, the greatest dry weight of both root and shoot was seen in aerated water culture, while weights were minimal in soil and polytherm. It is unfortunate that the plants were harvested at 8 weeks, so that we do not have any estimates of the weight of the grain which may be produced under these different conditions. One might guess, however, relying especially on comparative shoot weights, that the

water cultured plants might have the highest yield, followed fairly closely by vermiculite and then perlite grown plants. Also, although MacKey watered his plants every 2 hours, it is impossible to deduce what the affect of this watering interval may have had on the plants, and if other timing (and/or amounts) of the irrigation could have resulted in higher yield in the non-water culture plants.

Coopes (1977) examined root structure of Douglas-fir cuttings as a function of the nature of rooting medium which was used. He found that the most transplantable rooted cuttings developed in mixtures of sphagnum and vermiculite or perlite. His criteria for choice were not necessarily those which would be used if one were concerned with maximum yield, but his observation that the inclusion of sphagnum seemed to be most helpful suggests that the manipulation of soil organic content (and the nature of the organic material) may be of considerable importance.

In a study of uptake of iron by maize, Marschner and Azarabadi (1979) found a very large difference between plants grown in water and in sand culture when ferric hydroxide was the iron source (and nitrate nitrogen was used). In water culture, iron chlorosis could only be prevented by use of either very high concentrations of ferric hydroxide or of very low levels of phosphorus. Under either of these conditions, although the chlorophyll

was normal, the plants had a very low P content. By contrast, when conditions were the same, except that sand culture was used, ferric hydroxide was an adequate source of iron even when P was high. They concluded that the presence of (inert) surface against which the roots would grow was of importance, because in this "sheltered" local environment P could be reduced to low enough levels by uptake of the roots that Fe then was available from the ferric hydroxide.

The literature associated with soil-root interaction is large. Examples of additional sources (which give a glimpse of the complexity of the topic and entree to various parts of it) which may be consulted include: Harley and Russell, eds. (1979) which is the proceedings of a 1978 symposium on the soil-root interface and includes papers of a variety of subtopics; Nagarajah, Posner, and Quirk (1970), Cortez (1977), and Marshall (1979) who discuss the interaction of organic molecules in the soils with solid surfaces, especially those of clay; Tan and Nopamornbodi (1979) who discuss the beneficial effect of humic acids on the nutrient status of maize; Strickland, Chaney, and Lamoreaux (1979), who show that soil organic matter tends to reduce the phytotoxicity of cadmium (and of other heavy metals; Bremner and Banwart (1976) who plotted the uptake curves of soils for various volatile compounds of sulfur; and Barber and Gunn (1974) who found that maize and barley roots exuded greater

amounts of organic materials when grown in glass ballotini than when in liquid culture.

Plant defense mechanisms

Plants have a mixture of passive and active mechanisms which function against microbial invasion (not including the effects of the normal plant microbiota which will be discussed at length below). The following is a brief survey (which depends heavily on Agrios, 1978) of these mechanisms:

It should be made clear at the onset, because of the large variety of different kinds of plant pathogens and the concomitant wide range of characteristics of these pathogens, that plants cannot devise mechanisms any one of which will be completely effective against all attacks. (Agrios lists the plant pathogens as including about 8000 fungal, 200 bacterial, 75 mycoplasmal, and 500 viral species, plus a number of nematodes, a few protozoans, and so on.) From about 80 (wheat) to 200 (apple and potato) different pathogenic species attack individual species of crop plants.

Physical and chemical defense mechanisms are used by the plants to counter the invasive activities of the pathogens, and to inhibit those which are able to breach the outer barriers. Layers of various kinds of relatively inert substances, such as waxes and chitin, thickened

outer walls to the epidermal cells, mats or circlets of plant hairs, along with other kinds of morphological characteristics such as protective location of stomata, and so on, provide pathogens with greater or lesser physical barriers which must be overcome if invasion is to occur. Many of these plant characteristics vary with the nature of the environmental conditions under which the plant is growing (or has grown) -- for example, Cutter (1976) reports that the numbers and location of stomata of tomato plants are dependent on the level of the intensity of light during leaf morphogenesis. Under low light stomata develop only on the lower side of the leaf, while under higher intensities, about one fourth of them are produced on the upper surface of the leaves.

Upon the breaching (or damaging) of the physical defenses of the plant, other physical barriers may be produced. Cork layers, abscission layers, layers of (secreted) gums, and the blockages of the lumina of xylem vessels, for example, may be produced in response to pathogen presence; these will tend to isolate the pathogen-affected parts of the plant from the remainder, and may bring the spread of the pathogen through the plant to a halt. As a specific example, Ride (1975) observed rapid development of lignin in wheat leaf tissues near to where he had made experimental wounds, but only when fungi were inoculated into the wounds. Furthermore, the rate of lignification was more rapid when the inocula were of

pathogenic than when of non-pathogenic fungi. A related mechanism, in the functional sense, is the rapid necrosis of plant tissues which may occur near to the pathogen-infested tissues. By this "hypersensitivity" reaction, the plant may be able to isolate some of those pathogens which require access to living host cells for survival and reproduction; thereby the pathogen may be defeated. Once the hypersensitive reaction has been initiated it goes to completion (rapid and complete collapse of cells in the area, and necrosis of the affected host cells) even when the reaction-stimulating bacteria are killed with antibiotics as soon as the first signs of the reaction can be observed (Sequeira, 1979).

Some of the physical barriers to pathogen attack also act through their effect on the immediate environment of the plant such that the probability of attack is reduced. For example, one of the functions of the waxy and other hydrophobic layers on plant external surfaces is clearly that of reducing the time that a water film may cover those surfaces after they have been wet by rain or dew. Cook (1980), in a nice study, has shown that the wettability of peanut leaves is highly correlated with the rate at which the leaves are attacked by Puccinia arachinida. Wettability as it was determined by the characteristics of different strains of peanuts, and by the age of the leaves of each strain of peanuts (leaves become more wettable as they age) is highly correlated

with the rate at which those leaves become diseased. In addition, increasing the wettability of the leaves through application of water surface tension reducing agents also increases the rate at which the leaves are attacked by this rust.

As Royle (1976) and Agrios (1978) point out, structural defences of plants usually do not function alone; they almost always are complemented by biochemical defences. Frequently it is difficult to separate the two, for example when there is a hypersensitivity reaction as described above, it appears that in addition to the production of a barrier of non-living cells (which can in a very real sense be considered a chemical as well as a physical barrier, as the dead cell contents are chemically (and organizationally) very different from living cells), oftentimes anti-pathogen toxins are simultaneously produced. In any event, there frequently are chemical inhibitors of pathogen growth (or other pathogen activity) which are normally produced by various plants on some of their surfaces and/or in their cells. In some instances the pathogen relies on nutrient materials in the non-living environment, some of these are normal products of the environment around the host, and some may be derived from the host. For those which are products of the normal plant environment, their (possibly competitive) uptake by the plant may result in pathogen inhibition.

In instances in which the pathogen requires a host-produced nutrient or growth factor, adequate reduction of production of or release of the material may result in the avoidance of pathogenesis. As one example, Keeling (1974) examined the relationship between the amount of organic exudate produced by soybean seed and the degree to which the germinating seedling was attacked by Pythium ultimum and P. debaryanum. He discovered that susceptible strains produced twice as much exudate as more resistant strains. Other examples of this kind of relationship are numerous, and in many instances there is verification of the importance of the kind and/or the amount of the exudate through experiments in which additional exogeneous organic materials were added. This aspect of pathogenesis will be discussed at some length below (within the context of the effects of plant associated but non-pathogenic microorganisms and their effects on pathogen-host interactions).

Arinze and Smith (1980) give one of the many possible examples which might be cited concerning plant produced toxins which tend to inhibit pathogens when they discuss their experimentation on the furanoterpenoids produced by sweet potatoes. When the sweet potatoes are inoculated with any of the fungi, Botryodiplodia theobromae, Botrytis cinerea, or Cladosporium cucumerinum, four different terpenoids are produced. The plant's defense response to B. theobromae, which is the only one of these fungi which

is considered a pathogen of the sweet potato, was less successful than it otherwise would have been because B. theobromae is able to degrade the terpenoids more rapidly than could the other fungi, and because B. theobromae has greater tolerance to the terpenoids at concentrations which the sweet potato produces.

Many plants contain metabolic products, such as phenolics, which appear to have important anti-pathogen functions. Some of these are relatively unaffected in their concentration (and kind) by attack on the plant by pathogens, but there are a number of instances in which it is known that phenolic contents increase upon stimulation by the presence of attacking pathogens. In addition to the defensive effects of these (and other substances) which are found in many plants in the absence of pathogens, there frequently is a striking production of some additional anti-pathogen substances upon the breaching of the external defences of the plant by a pathogen. It appears that these materials, phytoalexins, are produced only in the presence of certain fungi (Agrios, 1978). At least in the soybean-Pythophthora megasperma var sojae system, the elicitor of soybean phytoalexin production is a 3-linked glucan which is common in the pathogen cell wall and which may be released into the medium in which it is growing (Ayers et al, 1976a, 1976b, and 1976c). The glucan elicitor stimulates the activity of phenylalanine ammonia-lyase in suspension

cultured soybean cells, and there is an accumulation of the phytoalexin, glyceollin, which is toxic to P. megasperma (Ebel, Ayers, and Albersheim, 1976). The production of phytoalexins frequently accompanies the hypersensitive reaction described above, with the result that at least two different approaches are taken simultaneously by the plant in its attempts to defeat the pathogen.

In addition to the above defense mechanisms which plants employ against the invasion of pathogens, there are several others which should at least be mentioned: These include the change in the chemical activities of the plant such that substrates which are sensitive to (enzymatic) attacks of the pathogen are replaced by substrates which are resistant. For example, complexes between pectins, proteins, and polyvalent cations which are much less sensitive than the original (normal) plant structural materials to enzymatic degradation by the pathogen may be formed. In addition, the plant may be able to inactivate (some of) the pathogen's enzymes as was discussed above (Arinze and Smith, 1980) and as outlined by Agrios (1978). It can be seen therefore that just as the plant has multiple defense mechanisms, the successful pathogen frequently will have a combination of mechanisms which it employs to overcome those defences.

Pathogen penetration processes.

After the dissemules of the pathogen arrive into close enough proximity of the potential host, there are a number of processes which may occur which permit successful attack on the host. (Some pathogen species have populations which live very close to or on the surfaces of their hosts for long periods of time; this will be discussed from a different point of view below, but it indicates that, for one reason or another, the host-penetration mechanisms of the the pathogen may not operate except under uncommon conditions, with the result that host and pathogen live at peace with one another for extended periods. This co-existance between host and pathogen is expressed in another way by Rovira (1979) when he says: "The presence of root pathogens in the soil-root interface may be more common than their absence".)

Both mechanical and chemical penetration mechanisms are used by pathogens. The former are not as common and/or important, on the whole, as the latter are (Agrios, 1978).

Because of the relatively small size of pathogens as compared to that of their hosts, the host can be thought of as having, in a limited but real sense, a mechanical advantage over the pathogen. Nevertheless, a number of fungi are able to exert adequate forces with their appressoria and associated penetration pegs to be able to force their way into host tissues. Usually these mechanical efforts at host penetration are accompanied by

the localized production of enzymes which bring about the degradation of some of the elements of the host tissues, thereby softening up the host for the mechanical attempt at penetration. One advantage to the use of some of these enzymes is that in addition to softening up the host, they may provide, through their activities, a nutrient supply which can be used by the pathogen. Of the structural defensive layers of plants, only the external waxes seem to be sufficiently inert to be resistant to all of the degradative enzymes of attacking pathogens (Agrios, 1978). The other substances which form barriers are attacked by cutinases, pectinases, cellulases, proteases, and so on.

According to Sequeira (1979), most pathogens have a very restricted host range, and these do not cause host death so rapidly that there is no time for (host) reaction to their presence and activities. This is summarized, in a sense by the ecologist's comment that well adapted parasites (in which there has been co-evolution between the parasite and the host) are "prudent". On the other hand, the pathogens which have a wide range of hosts frequently cause much more rapid damage to their hosts when they do manage to attack them (the hypersensitive reaction is especially likely when the plant is attacked by an incompatible pathogen). Between the pathogen and a host to which it has become well adapted, there appear to be a number of highly specific interactions which occur. For example, specific carbohydrate binding proteins

(lectins) of the host cell walls may bind strongly to carbohydrate molecules in the pathogen's cell wall. This kind of interaction also occurs between legumes and the specific strain of Rhizobium which forms (nitrogen fixing) nodules on the legume's roots. The situation is not clear, however, as Sequeira (1979) discusses experiments in which avirulent strains of Pseudomonas solanacearum become rapidly attached to the cell walls of the "host species", tobacco, and after attachment are rapidly broken down. On the other hand, virulent strains of the same bacterium remain free of this attachment and so are able to reproduce in the intracellular fluids. Sequeira goes on to point out that saprophytic bacteria also become attached to cell walls of tobacco, and then says: "Only those bacteria which can circumvent this defense response can continue to multiply".

It should be pointed out that Sequeira also expresses caution about the use of the Rhizobium-legume model to represent host-parasite interactions, and this point is reinforced by the comments of Yoder (1980), who discusses the great specificity of some of the other chemical interactions between host and pathogen. He suggests that toxins not only may be necessary for the pathogenicity which is observed (and in some instances such toxicity has been shown to be required), but also that host-specific toxins will recognize and affect individual cells of the host and even isolated organelles (chloroplasts and

mitochondria, for example) from the host.

On the other hand, Perombelon and Kelman (1980) in a review of the bacterial genus Erwinia, which may attack man and other animals as well as plants, have concluded that there is considerable lack of host-pathogen specificity in the activities of the soft rot bacteria. The common feature of the soft rot group (Erwinia, Bacillus subtilis, B. megatherium, B. polymyxa, Pseudomonas marginalis, and some strains of Pseudomonas sp, Clostridium, and Flavobacterium (those which produce pectolytic enzymes) is their production of pectic enzymes (particularly pectic lyases) and their ability to attack a wide variety of hosts.

Organic compounds which are produced normally by plants may have very great effect in the determination of the probability of attack of pathogens on the plant. These plant produced organic substances may serve the pathogen as chemical guidance systems, permitting the pathogen to move toward or grow toward the host. They also may be important, and in some instances are known to be extremely important, in providing the pathogen population with nutrients which it needs to remain large enough to effectively attack the host. Some of the recent work which has been done on these processes is that of Singh and Mehrotra (1980a and b), in which not only was the amount of carbohydrate and amino acid exuded by germinating seed of susceptible strains of gram (Cicer

arietinum) much greater than occurs in resistant strains, but there also was a striking correlation between the increase in the amount of carbohydrate and amino acid produced during germination (which increased as temperatures were experimentally increased), and the increase in mortality of seedlings from the attack of Rhizoctonia bataticola, which causes pre-emergence damping-off. This is similar to the pattern reported by Keeling (1974) in which soybean seed rot incidence is positively correlated with amount of seed produced carbohydrates. Keeling also found that the simple addition of a glucose coating to the seed before planting likewise increased seedling mortality from Pythium ultimum and P. debaryanum.

Natural elevation of levels of nutrients which can be used by pathogens also has been seen to considerably increase the incidence of attack of a number of pathogen species which gain entry to plants through leaf surfaces. Warren (1972), for example found that Phoma betae produced from 3 to 5% infection rates on leaves of Beta vulgaris when there was no pollen present, but under otherwise similar conditions, except for the presence of pollen on the beet leaves, the infection rate increased to around 88%. In a similar vein, Preece (1976) suggests that for some pathogens (especially for those which are facultative) pollen and/or the organic exudates of leaves are important determinative factors in spore germination

and plant infection rates. He includes very interesting data concerning the time required for the organic compounds which are released by the plant onto its leaf surfaces to build back up to "normal" levels after heavy rain (or washing). For the substances which are of importance to the nutrition of some pathogens, the renewal time is about 5 to 7 days, while the amount of time required for fungal inhibiting materials produced by the plant to return to their pre-rain levels is 7 or more days. Fokkema (1971) also observed that the presence of pollen on plant leaves resulted in an increase in pathogen population size and infection rate (and in population sizes of saprophytic species of several fungi, including pink and white yeasts). Preece suggested that it is the facultative parasites which profit from the presence of pollen and other organic materials on leaf surfaces, and goes on to say that the spores of obligate parasites do not need nutritional "assistance" on the surface of host leaves. Preece, however, points out that "our ignorance (of these matters is) immense".

With respect to a rather different kind of organic compound than usually is considered, Smucker and Erickson (1976), working in a mist chamber system in which it was possible to control the level of oxygen to which roots of peas were exposed, found that ethanol levels were important to pathogen growth rates. Fusarium solani f. pisi grew hardly at all on pea roots which were exposed to

air and therefore produced little ethanol. However when the roots were surrounded with an atmosphere containing only nitrogen and (30%) carbon dioxide, growth of the fungus (in this gnotobiotic system) was strikingly correlated with the amount of ethanol produced.

The extended review of Abeles (1973) discusses the many kinds of effects which ethylene has and may have on plants. The dynamics of the effects of ethylene on plants clearly are very complicated, but it is certain that a large number of kinds of plant processes involve ethylene in one way or another. Agrios (1978) also briefly discusses the implication of ethylene in plant pathogenesis. Swanson, Wilkins, and Kennedy (1979) outline something of the biochemistry by which ethylene may be produced abiotically in the soil and can be produced by a number of bacterial species frequently found in the soil and/or on plant surfaces (shoots or roots). They give data which suggest that (at least some species of) Erwinia, Pseudomonas, Agrobacterium, Xanthomonas, and perhaps even Escherichia coli may be capable of producing ethylene.

A large number of environmental factors affect the ease with which pathogens may reach the vicinity of plants and attack them with success. The amount of damage which they will do to the host also frequently depends on the conditions of the environment. A few of the many ecological responses which might be cited as examples of

these include: Take all of wheat (Gaeumannomyces graminis var. tritici) is greatly inhibited by pH of 5 or less (and of 5 to 6.5 in some soils), and pH at the root surface may be affected by the form of nitrogen fertilizer which is used (Smiley, 1979). For example, when ammonium was used, pH at the root surface is lower than when nitrate was added. On the other hand, Madsen and Hodges (1980) observed possible enhancement of attack of Drechslera sorokiniana and Curvularia geniculata on germinating seed of the grass Festuca rubra by an increase in the level of applied nitrogen, but did not find that the form in which it was added had an effect.

In a pot experiment, Graham (1980) obtained results showing that wheat which was grown in copper deficient soil was much more susceptible to powdery mildew than were plants grown in the same soil except that it had been amended with enough copper to overcome the deficiency. All of the wheat plants had about the same amount of mildew on their leaves when they were 6 to 8 weeks old, but by the time they were 17 to 19 weeks old, the plants growing in soil to which sufficient copper had been added had none, and the plants without copper still had high rates of infection.

Availability of water to plants has a very great effect on the rate by which they may be attacked by pathogens and the severity of the effects of any infection which may occur. Ingold (1978) discusses the effects of

water on spore liberation, Griffin (1978) shows how soil moisture levels affect survival rates and spread of several species of fungi, and Schoeneweiss (1978) outlines some of the interactions which may occur between the degree to which a plant is stressed for water and the probability that it will be attacked by various pathogens. As might be expected, different pathogens are more able to attack their hosts under different degrees of water stress. Schoeneweiss also includes an interesting discussion of mechanisms of attack of pathogens on their host plants. Also, with respect to water, Yarwood (1978) provides a very nice illustration which shows the comparative reactions of a number of pathogenic groups to high and low humidities (he gives diagrams for powdery mildews, viruses, rusts, downy mildews, anthracnoses, Botrytis cinerea, and Pseudomonas tabaci).

In addition, Beute and Benson (1979) report on the very great effect which the presence of a fauna of small soil animals may have on disease incidence. It is clear that the small wounds which the normal soil fauna will make on plant roots provide for entry of pathogens which otherwise might not be able to invade their hosts. They discuss a fascinating instance in which the soil mite, Siteroptes reniformis requires the presence of the fungus, Nigrospora oryzae for its normal growth and reproduction. The fungus, which is the causal organism for lint rot of cotton, in turn is aided by the mite in its dissemination,

inoculation into cotton, and in its early growth.

Finally, in addition to all of the above, it is known that a number of plant auxins, gibberellins, and cytokinins may be either produced by plants in greatly increased amounts as a result of pathogen attack, and/or they may be produced by the pathogen itself. In some instances these may be important in the promotion of the pathogen's attack on its host.

Plant production of microorganism-usable substrates.

By the roots

The microbial populations normally found around the roots of plants are supported by the nutrient content of dead roots, root hairs, and root cap cells, by the non-cellular organic compounds which are exuded by plant roots, and by organic compounds which are leached out of the leaves and other aerial parts of plants and brought into the soil by rain (and in some instances by dew) runoff from the plants. In addition, of course, there frequently is incorporation of dead pieces of the aerial parts of the plants into the soil, but these inputs are not of great import in our immediate context here.

The compounds of greatest interest to the possible problem which is under consideration here are those within the smaller roots and root hairs, and the non-cellular

organic materials which are exuded from root and shoot surfaces. The reason for this is that the larger plant parts could be removed from the system relatively easily, but as long as the plants are growing they will maintain a continuous production of the smaller plant parts and of exudates, and it will be impossible to remove these from the matrix of the living plant. Therefore it behooves us to consider what the implications of the continuous addition of this kind of material at the plant surfaces may be with respect to microbiological activities.

Cellular materials.

Great interspecific differences occur with respect to the amount of root material produced and then "allowed" to die by different plants. The most obvious kind of difference exists between annuals and other species which have longer lives and keep many of their roots throughout life. In six native grassland areas of North America, Warembourg and Paul (1977) used carbon 14 to estimate carbon flows, and concluded that half of the carbon content of a given sample of roots is lost in about 107 days. The losses were from root respiration, exudation of organic materials, and decay of the roots which had died, but (even though there are some problems with the paper) the fact that about 43% of the total carbon fixed by photosyntheses is deposited in the roots, and half of this is lost from the root system in less than 1/3 of a year,

shows that considerable loss occurs by this route. Because there is no long-term increase in the organic matter content of these soils, much of this loss (that which is not direct root respiration) must have been as a result of the activities of the microbiota living in, on, or near to the roots. Sauerbeck (1979) also provided data showing considerable total input to the underground parts of plants, and the loss of much of this to decomposition. In wheat, corn, and mustard, he demonstrated, using the carbon-14 method, that the amount of plant root substance formed and then broken down before harvest was greater than the amount of plant residue (roots) in the soil at the time of harvest. Therefore, the loss to the microbial populations of the roots and soil was greater than the amount retained in the roots. Sauerbeck points out that these plants may use about $1/4$ of their photosynthetic assimilation for the production of roots, and that only a relatively small proportion of this is used in maintaining them, therefore "secondary microbial decomposition represents the bulk of it".

At a somewhat finer level of consideration, Clowes (1971) estimated the output of root cap cells of maize to be on the order of 10,000 cells per root per day. The rather near term fate of these cells then is to become nutrient sources for the microbiota. Griffin, Hale, and Shay, 1976, examined culture solutions in which axenic peanuts had been growing, and observed that many of the

root cap and other cells which the plants sloughed off contained very little cytoplasm. They measured the C:N ratios of the particulates from their cultures and found that this ranged from 9.0:1 in plants growing in relatively nitrogen-rich Hoaglands solution (1/4 strength) to 18.9:1 after the plants had been transferred to culture medium lacking nitrogen and kept there for a while. Their measurements provided an estimate that about 0.15% of the root content equivalent was sloughed off per week under these conditions.

Root hairs, which are extensions (usually from about 100 to 1000 micrometers long, and from about 5 to 17 micrometers in diameter), usually arise from the epidermal cells of roots. There is argument concerning their function, which may be water and/or nutrient uptake. The number of these root hairs varies considerably as a function of plant species, and also with environmental conditions under which a species grows. From 50 to 100 per mm of root length may occur in grasses, and in loblolly pine only about 2 per square mm are found (Nye and Tinker, 1977). Bohm, 1979, reviews methods of study of roots, and along with Nye and Tinker, gives good entree to the literature. When root hairs die, which may be from days to months after they are produced, they provide large surface areas for the microbiota to invade and commence the decay processes. In sum, there are a number of different sources within root systems which provide for a

continuous output of finely divided cellular organic matter in a form which is readily utilized for the nutrition of the microbiota of the root zone.

Root exudates.

In addition to the cellular materials which plants make available to their associated microbiota, there are a number of non-cellular exudates which are produced by the roots and which clearly play an important role in the complex of relationships observed between plants and their normal, generally non-pathogenic, microbial associates. At least some of these exudates are produced by active secretion, and an examination of the literature suggests that the rate at which passive loss occurs could be reduced by relatively simple evolutionary changes in the physiology or structure of the plants. The conclusion, therefore, seems reasonable that the exudates are part of a co-evolved mutualistic "bargain" which plants have made with their non-pathogenic microbial associates.

Hale, Moore, and Griffin (1978) have provided a good and recent summary of our knowledge of exudates of plant roots, and Hale and Moore (1979) give a summary of work between 1970 and 1978 in the field, with concentration on the factors which affect root exudation. Most plant species produce water-insoluble polysaccharides which form layers of varying thickness on the younger parts of their roots. In addition, other polysaccharides, sugars, amino

acids, proteins, growth promoters and inhibitors, attractor and repellent chemicals, chelators, solubilizers, and compounds which affect pH and the aggregation of soil particles, and no doubt chemicals with other functions are exuded by plant roots. Different species, and within species, different parts of the root system produce different kinds and amounts of exudates. In addition, many environmental factors interact with the plant's roots and shoots to influence kind and amount of exudation. Among the factors affecting exudation are temperature (level and rate of change), light, water availability, mineral nutrient levels, oxygen concentration, and the activities of the associated microbiota (see Hale and Moore, 1979 for a good review). These factors operate through their influence on cell membrane permeability, and by affecting flux ratios via change in source-sink relationships within the plant and between the plant and the rest of the world.

If the beginning of the modern examination of the exudates of plant roots were chosen, it might well be marked by Vancura's 1964 paper. In that, he describes his experiment in which he grew axenic wheat and barley plants, and while they were still young, stressed them for water. After that he observed the exudation of water-soluble organic compounds from their roots. The results are affected by the water stress treatment (a matter which will be discussed below), nevertheless,

Vancura listed a number of the compounds which were exuded by the plants, and the pattern is similar to many which have been seen since. He observed a variety of sugars (mostly oligosaccharides), organic acids, amino acids (18 and 15 from wheat and barley, respectively), and a total of 9 phenolic substances. Vancura and Horadlk, 1965, in a continuation of the original work, determined the composition of the root exudates of turnip cabbage, cucumber, red pepper, and tomato. In the pepper and the tomato, in addition to simply examining the various kinds of molecules produced, Vancura and Horadlk compared the amounts and kinds which were exuded by young and by fruiting plants. All of these plants (including the different ages of the pepper and tomato) exuded many amino acids (from 17 to 21), a moderate number of organic acids (4 to 7, except for cucumber which produced only 2), a moderate number of sugars (8 to 10, except for turnip cabbage which produced only 2 and fruiting pepper and tomato which released 2 and 3 respectively), a couple of non-acid and several acid phenolic substances. In addition to its interest as an early work showing something of the variety of organic substances released by roots, their data illustrate the change in the spectrum of compounds released as plants age and begin to fruit. The pepper and tomato, for example, exuded 10 and 8 different kinds of sugar as young plants, but as mentioned, only 2 and 3 of them, respectively, as fruiting plants.

Rovira (1969) was also among the pioneers in work on plant root exudates; in the review cited, he listed 9 sugars (+ "oligosaccharides"), 19 amino acids, 10 organic acids, 2 nucleotides, 3 enzymes, and flavone in the exudates of wheat roots. Smith (1976) found that trees (at least Betula alleghaniensis, Fagus grandifolia, and Acer saccharum) of the northern hardwood forest produced exudates which are comparable to those of the plants discussed above. There were, of course, interspecific differences, and organic acids were the most abundant component of the exudate, but these results suggest that all kinds of vascular plants probably exude substantial quantities of a variety of soluble organic compounds. In the trees, Smith concludes that the amount of exudate is great enough so that it plays at least a small role in intrasystem nutrient cycling.

Odumfa (1979) considered (as have a number of others) the exudates of seed; in a comparison between the amount and kind of organic substance released by seed and root, it turns out that the exudate of the seed is much richer than that from the root. Odumfa also compared exudates of sorghum with those of cowpea, and found that both with respect to seed and root, the production of the legume was greater. It may be especially important that some of the amino acids released in relatively high amounts by the cowpea were the only sources which the fungi Fusarium solani, F. oxysporum, and F. semitectum could use for

their nitrogen supply. It was also of interest that the high level of glycine in the cowpea exudate has an inhibitory effect on Rhizobium. In a 1980 paper, Odumfa continues the comparison of sorghum and cowpea, confirming a number of the statements made above, and adding (among other things) the information that under comparable conditions, cowpeas produced 6.2 micrograms of carbohydrate while sorghum produced 1.6 micrograms. He makes the comment that the observed difference in amount of exudate from sorghum and cowpea probably explains (at least part of) the greater affect that the latter has on its rhizosphere.

Bokhari, Coleman, and Rubink (1979) examined the exudates of short grass prairie plants, the grass, blue grama (Bouteloua gracilis, and the fringed sagewort (Artemisia frigida). They give pattern and relative amounts of sugars (soluble and nonsoluble) and amino acids produced by axenic blue grama, and found in the rhizosphere and bulk soil of both species. They report lower levels of sloughing of root cap cells, etc., than Griffin, Hale, and Shay (1976) did for peanut, but found that blue grama sugar exudation increased from 6mg/g plant dry weight/30 days in seedlings to 32mg/g for mature plants (which of course, weighed much more). They also found that, in nature, the rhizosphere soil of both species contained more soluble sugars than did adjacent bulk soil, while the reverse was true in nonsoluble

sugars; amino nitrogen (both soluble and nonsoluble compounds) by contrast was higher in the bulk soil than in the rhizosphere soil of both species. In addition, there were more polyphenols in rhizosphere than in non-rhizosphere (bulk) soil of both species, but it cannot be determined if either these phenols or the traces of terpenes found by Bokhari, Coleman, and Rubink had the inhibitory affects that Rice (1974) found grassland successional stages to have on nitrogen fixation -- probably on Rhizobium and/or Azotobacter. (These authors claim evidence against such inhibition, but their logic does not hold in this instance.)

Kraft (1974) examined the production of reducing sugars and phenols by germinating seeds and seedlings of peas. He then exposed these young plants to several fungi (Fusarium and Pythium) which cause root rot in peas, and was unable to correlate the amount of the sugars or of the phenols with the resistance of the various pea cultivars to these fungi. He concluded as a result, that there must be other compounds, so far unknown and perhaps undetected, which confer the various levels of this resistance on the different strains of peas.

Stotzky and Schenck (1976) observed several kinds of oxidizable volatile compounds to be evolved by germinating seeds of several species of plants. Some of these were aliphatic aldehydes (but formaldehyde made up only a small proportion of these). That these compounds are the result

of the plant's (seed's) metabolism is suggested by the experiment in which killed seed failed to produce the aldehydes. Stotzky and Schenck speculate that these volatile compounds may stimulate microorganisms, but have no evidence to directly support this. Vancura and Stanek (1975) investigated the sources of the compounds (or precursors thereof) which are secreted by roots of bean seedlings, and found that while 462 mg per 1000 plants of exudate was produced normally, only 292 mg were released by plants which had had their leaves removed, and even less, only 201 mg, was produced by seedlings which had been deprived of their cotyledons. Not surprisingly, different components of the exudate responded with different pattern of change to the various treatments. Vancura and Stotzky (1976) also examined the volatile compounds released by germinating seeds and seedlings. They observed peak output of a number of compounds (which were not produced by killed seed) as early as 20 to 48 hr. after wetting of the seed. Within a mixed group of species (4 pine, alder, cotton, and 8 vegetables) they observed production of ethanol by all species, and of chemicals of the following list by 3 or more of them: methanol, acetaldehyde, formaldehyde, formic acid, ethylene (in 4 out of 4 tested for it), propylene, and other unidentified organic substances.

There is a Psuedomonas sp. which uses the formide produced by the action of the pathogenic fungus

Gleocerospora sorghi from the cyanogenic glycosides of the plant host, Sorghum. This is not really the result of the simple production of an exudate by the plant, but is included here to give an example of some of the complex kinds of interactions which will have to be taken into account in the final analysis of the problem under consideration here.

Layers of polysaccharides of various thicknesses and characteristics have been reported on the roots of a number of plants. Clowes (1971) described golgi vesicles in root cap cells of maize which, with about 3 hr. cycles, produced and dumped water-insoluble carbohydrates to the exterior. Sprent, 1975, in a simple experiment, found that more sand stuck to the roots of soybean after it had been exposed to water stress, and attributed this occurrence to an increase of the production of mucilaginous carbohydrate by the roots in response to that stress.

Leppard (1974) observed microfibrils of secreted polysaccharide on the roots of wheat with an electron microscope, and Dayan, Banin, and Henis (1977) presented some nice electron micrographs which illustrated mucigel layers around barley roots. The characteristics and thickness of these layers differed from one part of the root system to another. Leppard observed tufts of polygalacturonic acid and pointed out that this may increase the plant's absorptive area and may also have

been responsible for the development of the capacity to produce polygalacturonase by some of the rhizoplane microorganisms. Polysaccharide layers are frequently observed to have covered the root from its tip through the root region of the root hairs. In some areas these layers have fibrillar character in which there are alternating layers which are concentric to the root. The initial layer(s) of polysaccharide produced by the roots are variously corroded by and added to by the bacteria of the rhizosphere; as older and older roots are examined the thickness and continuity of the layer(s) are reduced. A number of bacteria were seen scattered through the mucigel, and Dayan, Banin and Henis discuss the necessity of keeping these (and other) bacteria from being able to attack the mucigel during water extraction if the activity of the bacteria (especially the lysis of the mucigel) is not to interfere with results. They found that in the presence of the bacterial inhibitor, chloramphenicol, little of the root mucigel was removed by 10 min. of exposure to warm water (except that some of the sugars and proteins were removed), and that while there was a definite loss of bulk from the mucigel layer after 90 min., it took 3 hr. of shaking to remove most of it from the roots (and some still remained).

Paull and Jones (1975a and b, 1976) provide confirmatory and additional details concerning (maize) root exudates in their series of biochemical studies of

insoluble polysaccharide production by the plant roots. They concentrate on the intracellular location of radio-fucose in the roots and conclude that the dictyosomes are the sites of accumulation of fucose which then is secreted to the exterior of the cell where it, along with galactose, makes up about 69% of the neutral sugar of the root's polysaccharide slime. (Fucose is especially useful to this kind of study because it is metabolised by the plant slowly if at all.)

Martin (1975) brought the attention of those studying this matter to the fact that some (and perhaps sometimes, much) of the carbohydrate around or near to the roots of plants probably was of bacterial rather than of plant origin. His procedure was to label the plant with carbon 14 and to then examine the kinds of materials removed from the roots of wheat, clover, and rye by leaching with water. The leachate was labeled, he claimed, because the bacteria had taken up labeled compounds which had been exuded by the plants, and used these to manufacture the carbohydrates which subsequently were removed by the water. Warembourg and Billes (1979) presented evidence from a more sophisticated experiment. In a nice piece of work, they grew wheat axenically in water culture, and pulse labeled it with carbon 14 (for 1.5 hr. in the light). They then were able to follow the course of the labeled carbon as photosynthate manufactured with it was taken to the roots and used in the respiration of those

roots and as exudate. There was a peak in output of radiocarbon dioxide immediately upon the labeling process, and another much smaller one the next day (the root respiration was higher during the day than at night). In similar plants, except that they were not axenic (a culture of a bacterium from a grass rhizosphere was used), the first peak was the same, but the second day's peak was much higher, and on the third day there was an additional small peak (which was not seen at all with axenic plants). Warembourg and Billes hypothesize that the heightened second day peak in the presence of bacteria is the result of the microbial population's activities, as the population size had by then grown large enough that it could rather rapidly metabolize the plant's exudates. The molecular weight of the carbohydrates present in the liquid root culture medium during the first (root) output pulse of carbon dioxide was low (90% less than 700); by the second day, in the culture containing the bacteria, and associated with the larger second peak, the dissolved organic component was of considerably higher molecular weight (1/2 to 2/3 was over 700, and of this, about 1/2 was over 50,000). This latter represents the bacterial production (polysaccharide produced by this bacterium had a molecular weight of about 51,000). Warembourg and Billes suggest that the peak which was seen on the third day (only in the bacteria containing cultures) was the result of their beginning to use the larger molecular weight material which had previously been produced by

bacteria (which used low molecular weight plant root exudate as their nutrient resource).

The following sections will outline the affects which various environmental factors have on exudation by plant roots. There frequently is considerable change, both qualitative and quantitative, in the exudation of roots as root and as plant become older. Van Egeraat (1979), for example, points out that at least in several legumes (cowpea especially), there is a difference in the composition of the exudates produced by root tips and by older roots. Exudate from older roots has a composition which is very much like that of the soluble fraction of the root, suggesting that the exudate is produced as a result of damage to the root tissues (cells) by the rupturing effects of emerging lateral roots. This same view is accepted by van Vuurde and Schippers (1980) who examined the number of nonliving cells along the length of 10 day wheat roots (as measured by the presence of non-stainable nuclei). They suggest "rupture of some epidermal and cortical cells" as the mechanism which releases increased organic materials which are responsible for the increase in bacterial populations which can be observed in this lateral root producing region of the seminal root.

On the other hand this suggestion that cell damage is produced by emerging lateral roots was made some time ago, and thereafter, as a result of autoradiographic work which

appears good, McDougall and Rovira (1970) arrived at a different conclusion. They used wheat and provided data consistent with the hypothesis that the exudation which supposedly came from the damaged roots came rather from the relatively very high exudation from the tips of the new roots while they were forcing their way through the older root to the surface.

A change in amount and composition of exudate with plant age and life history stage has been demonstrated by a number of observations and experiments. Smith (1970), found that the amount of sugar exuded from seedling maple tree roots was about 5 times that exuded (per unit root weight) by unuberized tips of mature roots, but that the amount of amino acid produced by the mature roots was about 4 times that of young roots, and that there was also greater exudation of organic (non-amino) acids by older roots (by a factor of about 6). Juo and Stotzky (1970) detailed changes in the kind and amount of protein exuded by roots of sunflower, pea, corn, and dwarf corn with age. According to Matsumoto, Okada, and Takahashi (1979) there are changes in corn root exudates with plant age with respect to nitrogen compounds and sugars which are soluble and are insoluble in ethyl alcohol. These all had rather striking peaks, when measured as amount exuded per gram plant material, about 11 days after germination of the plants. Evaluation of the total amount of these materials produced by the plant (from the curves provided) shows

that after this peak of high output per unit plant mass, there is a decline in the total output, but that as the plant grows, exuded material produced per unit time increases until it is largest (at least for ethanol soluble substances) shortly before heading; thereafter it declines somewhat. Hamlen, Lukezic, and Bloom (1972a and b) followed changes in exudates of axenic alfalfa plants, and describe a reduction of the amount of the exudate produced (per unit total root weight) as the plants aged. They also observed an increase in the amount exuded per unit root weight with an increase in the severity of clipping of the plant tops, although there was a decrease in the amount of exudate per unit total plant weight. Work by Vancura and Horadlk (1965) on differences in exudates of young and mature peppers and tomatoes, and by Vancura and Hanzlikova (1972) on differences between seed and seedling exudates, which were cited earlier also should be mentioned again in the current context.

The early literature contains a number of suggestions that the mechanical effects resulting from the pressures generated by roots as they force their way through solid might have effects on root exudation. That these pressures do influence exudation was shown by Barber and Gunn (1974) when they grew axenic wheat either on glass ballotini of different sizes or under unrestricted conditions. In maize they found that roots developing in a matrix of ballotini were shorter than those which grew

unrestricted in simple liquid culture. Also, when the size of the ballotini through which the roots had to grow was 1 mm, and the required pressures greater than with ballotini of 3 or 6 mm (or with no ballotini), the amount of carbohydrate exuded was increased by a factor of about 4.5 and that of amino acid was increased by somewhat over 2.5 times. (With 1 mm ballotini the roots must push the glass beads aside to penetrate the medium while with 3 or 6 mm ballotini the inter-bead spaces are large enough to accommodate the roots of the young plants of the experiment.)

The amount and duration of the light received by the shoots of plants is well known to have effects on the delivery of photosynthate to the roots and thereby to the rate at which exudation occurs. This phenomenon will be discussed below in the context of nitrogen fixation by mutualistic bacteria, especially by Rhizobium living in nodules of legumes (where it has been most studied). For now, the example provided by Barber and Martin (1976) will serve: If 3 week old wheat plants are provided with 12 hr. light periods (per 24 hrs.) they produce 508 mg of organic exudate; 788 mg is produced, everything else being equal, by plants receiving 16 hr. light periods. These data were obtained with axenic plants, and the increase in exudation usually seen in plants in non-sterile soil occurred. It was slightly less (141% rather than 155% more) in the longer compared with the shorter light

period. This interaction between exudation and the microbial biota of the rhizosphere will be discussed in more detail below.

Temperature influences the amount and kind of root exudate produced. Vancura (1967) reported that there is a general increase in the amounts of amino acids and sugars with an increase in temperature when the range of temperature was well within the plant's normal limits. There are also changes in proportions of materials exuded, with changes of some materials running counter to that of the overall pattern (for example there was a decrease in maltose and fructose output on change of temperature from 19 to 28° C). Martin (1977) grew wheat at 10 and at 18° in sterile soil for 23 and 26 days respectively. There was somewhat over 6 times the organic exudate deposited in the soil under the higher of these temperatures. If the sizes of the plants (root plus shoot dry wt.) is taken into account, the fact that the plants were 3 times larger at the higher temperature means that the increase of exudate is to twice what it was (on the basis of plant weight) at the lower temperature. Martin and Kemp (1980) examined the exudation of the roots of 11 cultivars of wheat, and found that there were no significant intraspecific differences. They did find slightly greater exudation at 15 than at 10° C, but although this conclusion probably is justified, their procedure could have been better.

In addition to the general effects of temperature level, there are those of rapid and extreme change. Seeley and Kammereck (1977) exposed apple trees to "light frost" conditions after vegetative growth had begun. They did not observe exudation from the plant's roots, but found that the assimilation of carbon within the plant was drastically curtailed, even though there were no visible symptoms of damage to the plants. It seems reasonable to suppose that root exudation probably was greatly reduced as the photosynthate manufacturing mechanism appeared to be paralyzed. Vancura's 1967 paper includes data which illustrate effects of a temperature shock (which was somewhat less extreme than that used by Seeley and Kammereck). He found that maize produced considerably more exudate after cold shock (even though here, as with the apple trees, there was a substantial inhibition of the plant's growth). Vancura speculated that the increase in the output of the corn was the result of a change in the permeability of the cells of the roots. However, under most natural conditions the effects of short, sharp temperature changes will be considerably buffered by the roots being in the soil, frequently at an appreciable distance below the surface, where the changes will be much muted. This is especially true of larger plants. The roots of plants which are unfortunate enough to be growing in pots, unless special efforts are made, may be exposed to much greater (and more rapid) temperature fluctuations than normal to them.

Vancura (1964), as was mentioned above, used a moisture stress to increase the yield of exudate from the roots of young barley and wheat. Sprent (1975) observed increase in the mucigel on roots (near their tips and in the region of the root hairs) of soybeans as the amount of water stress to which the plants are exposed was increased. Martin (1977) reported an increase in organic carbon released by wheat roots with increase in water stress. He suggested that both production of mucilage and lysis of root cells are increased by this kind of an environmental stress. He did not, however, take into account the fact that he was not using sterile soil (and plants) in his experimentation. It may be that his results are correct, but because the microorganisms well could be affected by the water stress in such ways that the results observed might be produced by their change in activities, the details of the results of the experiment are not as useful as one would like.

A number of studies show that there is an effect of the mineral condition of the soil or medium on the exudation of organic materials from roots. Ayers and Thornton (1968) found more ninhydrin responsive substances to be released from roots when the culture medium was aerated with a mixture containing 0.5% carbon dioxide rather than with one with low carbon dioxide. The 0.5% is closer to the content of the normal soil atmosphere, and this, as Ayers and Thornton suggest, is probably

responsible for the results observed. Bowen (1969) worked with axenic Pinus radiata seedlings, and observed that after exhaustion of the seed's supplies (about 2 weeks after germination), phosphorous deficient culture solution resulted in an increase in the rate of root exudation of amino acids to about 2.5 times what it was in nutrient sufficient medium. On the other hand, when the medium was nitrogen deficient, the amino acid exudation was only about 1/4th of what it was in sufficient media. This appears to be an adaptation towards the promotion of greater mycorrhizal development under conditions of low phosphorous (and high nitrogen) in which these mutualists would be most helpful. Mycorrhizal mutualism will be discussed at greater length below. Shay and Hale (1973) and Hale (1978) report on the effect of calcium concentration of the culture medium on the exudation rate of peanut plants. Roots, pegs, and young fruit all responded differently to different calcium levels. Use of a variety of concentrations down to 10 mg Ca/L provided evidence of greatest exudate release at 10 mg/L (sugar exudation at 10 mg/L of Ca was 4 times what it was at 50 mg/L). In addition, Vancura and Stanek (1975) found that bean roots exuded twice as much organic material in distilled water than in a Hellriegel nutrient solution.

In a discussion of the interactions between microorganisms and plants, Rovira in 1972 commented that "at least 20% of the production potential (of plants) is

lost simply to satisfy an unfavorable microbial situation". Barber and Martin (1976) provided information of the degree to which microorganisms may stimulate the exudation of organic materials from roots when they worked with wheat and barley and found that the per cent equivalent of total plant material which was released in 3 week plants was about 7 to 9% (depending on light level - - it well might have a wider range) for wheat in sterile and 18 to 20% for non-sterile soil, while for barley the estimates were 13% and 25% for the sterile and non-sterile soil, respectively. Foster and Rovira (1976) discuss the nice electron micrographs which they have taken of roots and their immediate vicinity. One of the striking aspects to these data is that (at the flowering stage of wheat) older roots show that they have been considerably damaged. It appears that there is an invasion of the epidermal and cortical cells of the root by microorganisms, and this is accomplished by the microorganisms via localized lysis of the cell walls which they bring about. Considerable organic material may be lost from living roots in this way. Martin (1977a) also points out that there may be lysis of the walls of root cells without apparent penetration of the cell by the microbes. Autolysis also may occur, and in fact, may be the cause of "a major loss of root carbon". Foster and Rovira (1978) provide beautifully detailed transmission electron micrographs, and with these as guides, developed a useful classification of various of the different

micro-ecological zones near, on, and in Trifolium roots.

It is clear from the above discussion that there are many kinds of organic materials which plants produce at (or in) the surfaces of their roots. The ease with which these may be used by the microorganisms associated with the roots for their nutrition varies, but many of the root-produced substances (both cellular and non-cellular) are readily available to the microbes and have high nutritive value to them.

An effective example which makes essentially the same statement is that given by Sauerbeck and Johnen (1976), who studied the fate of the carbon which was delivered as photosynthate to plant roots. In mustard and wheat they found that the amount of root material present at harvest time represented only from a third to a fourth of the total organic matter which had been delivered to the roots during the season. There was some root-derived organic matter in the soil which was not detected by the methods usually used to separate root residue from the soil, and taking this into account, there still was a mineralization during the season of about three times the equivalent of the end of season root material. Furthermore, the respiration of the roots themselves was responsible for the production of only about one fifth of the carbon dioxide which was produced in the soil.

As will be discussed in some detail below, however, plants usually have greater yield in the presence of a microbial community, even though their root exudation is considerably increased by these microorganisms.

Leaf (and shoot) exudates.

The aerial parts of plants frequently have accumulations of organic substances on their surfaces on top of the cutin and wax layers which are really parts of the leaf. Most of these come from the plant, and they may have effects of encouraging or discouraging the development and maintenance of microbial populations of the plants' surfaces (these populations will be discussed later). Carbohydrates, amino acids, phenols, and other kinds of compounds are exuded to the plant surface. A number of plants have specialized structures, the hydathodes, through which liquid is discharged from the interior to the leaf surface. These frequently are found on leaf margins, especially at leaf tips, and sometimes one can observe a droplet at the leaf's tip or a series of droplets around the edge of the leaf which have come, carrying dissolved organic materials, to the surface of the leaf. Wheeler (1973) also found that wheat guttate contained materials which appeared to be gibberellin, and that ethanolic washings of tips of dry wheat leaf tips also showed cytokinin activity.

Also, especially when the leaf surface is wet, organic materials may move through the leaf surfaces. Tukey (1970) provided a review of the variety and amounts of organic materials which are leached by rain (and its experimental analogues) from plants. In addition to the carbohydrates, amino acids, and phenols referred to above, leachates of plants may contain vitamins, growth substances, and other organic substances (and a number of plant inorganic nutrients including Ca, K, Mg, Mn, Na, P, Fe, Zn, Cl, and so on). Amounts of both organic and inorganic materials which are observed to be leached from plants under natural conditions are great enough to have considerable impact on the nutrition of the plants and on the mineral cycling which occurs in the ecosystem. The amounts of materials which may be lost by rain-leaching are greater than commonly realized - young leaves, for example can lose as much as 25% of their supply of Na and Mn in 24 hr. Young beans also have been observed to lose 6% of their organic content in 24 hr., and apples have been estimated to lose as much as 800 kg per year per hectare (of carbohydrate).

Godfrey (1976), in a more recent review of plant leachates, points out that dew can have appreciable quantities of organic material dissolved in it. This no doubt comes from the previously dry surface of the leaf, and measured quantities include 19 and 16 micrograms per ml of carbohydrate and amino acids for lettuce, and 74 and

52 micrograms of those classes of compounds, respectively, for watermelon dew. Preece (1976), after a comment that "our ignorance (about these matters is) immense", presents a very nice study illustrating the different rates of buildup of carbohydrates and of a fungal inhibitor on dry leaf surfaces (more detail of this will be given later). Preece (1976) follows Fokkema (1971 a and b) and Warren (1972) in pointing out that organic particles can be deposited on aerial plant surfaces from the atmosphere, and that some of these can add appreciably to the microorganism-available nutrients found there. Pollen grain deposition appears to be especially important, and as will be discussed at greater length below, may improve the probability of a pathogen being able to mount a successful attack on the plant. In sum, then, there are organic materials, in addition to the plant structure itself, which are found frequently on plant surfaces, and the kinds and concentrations of these are sufficient to support a continuous microbial community and to affect plant disease attack success rates.

The normal microbiota of plants.

The communities of microorganisms living in association with plants are complex and usually are composed of enormous numbers of individuals. The preponderant majority of these individuals usually are in non-pathogenic species, but it is probable that there are

almost always at least a few individuals of pathogenic taxa present. Rovira, for example, supports this commonly held view with the statement: "The presence of root pathogens in the soil-root interface may be more common than their absence."

The difficulties in the systematics of microorganisms, especially in groups which are not pathogenic, should be emphasized again at the beginning of this section. More will be said about our ignorance of the systematics and ecology (physiology) of plant-associated microorganisms below; emphasis of this ignorance is contained by clear implication in Billing's (1976) comment to the effect that the only reason that we know as much as we do about the genus Erwinia as we do is that originally it was thought to contain pathogenic and therefore economically important species. It also should be mentioned that there are "non-pathogenic" species which apparently, at least under some conditions, cause significant damage to plants (Bowen and Rovira, 1976; Cother, Darbyshire, and Brewer, 1976; and Lynch and White, 1977).

In the discussion below of the normal microbiota of roots and of the aerial parts of plants, only a sampling of the information in the literature is possible here. There are a number of papers which list various species or various groups in surveys of some of the organisms associated with plants; compiling a "grand list" from

these would not be very useful to the purposes of this paper. This section will concentrate more on some of the plant and environmental factors which influence the microbial populations associated with plants, and the next section will be directed more at a discussion of the nonpathogenic effects that these microbial communities have on "their" plants.

Root microbiota

At the most gross level, a number of workers have examined the total of the activities of the microbiota of various soils. In addition to the conclusions of Sauerbeck and Johnen (1976) concerning the relatively large contribution to the soil's production of carbon dioxide which must come from the respiration of the microorganisms, Wani and Shinde (1980) followed the changes in soil microbial community structure following the incorporation of aerial plant parts into the soil. In a similar study, except that the point of interest was somewhat more narrow, Elliot et al (1979) examined the influence of added plant material on the colonization of the rhizoplane by bacteria. In addition to finding out that greenhouse pot experiments provided for poor prediction of patterns which would develop in the field, they observed greater numbers of bacteria on the roots of plants which had had straw around them on the surface, but no straw incorporated into the soil, than in other

treatments. These are meant to be only illustrative examples, as there are many other similar reports of studies on two of these topics in the literature, especially on the last - the effects of incorporation of plant material into the soil.

In another direction, Anderson and Domsch (1973) examined microbial dynamics in (only) one kind of agricultural soil. They used inhibitors which were selective and thereby were able to obtain separate estimates of the contributions which bacteria and fungi made to the total respiration of the microbial community, and they found that these were 78% and 22% for the bacteria and fungi, respectively. These proportions are, of course, sensitive to environmental conditions; moisture levels, and both the timing and the composition of added nutrients to the soil are among the more important of these.

The size and activities of the microbial populations also will be related to the efficiency with which the microbial species can use available nutrients. Veldkamp (1975), to give one example, reports on efficiency of production of Pseudomonas oxalaticus when degree of carbon limitation was controlled by the amount of glucose added to the experimental system. He found a cell mass yield of about 0.5 when glucose was high enough to provide for a specific growth rate of 1.0 per hour, and calculated that the metabolic cost which was involved was about 0.1 of the

glucose used. The yield efficiency, not surprisingly, dropped off when glucose was made available only in lower concentrations. At levels which permitted a specific growth rate of only 0.01 per hr., the cell yield was 0.14.

One of the several direct measures of the degree to which plant-produced organic materials determine the size and structure of microbial communities on plant roots is to survey the populations on (or very near to the surface of) the roots, and to compare these data with similar information concerning the flora of the (bulk) soil. Gray and Williams (1971) provide numbers which are useful in this way (their table 19). Their root:soil (R:S) ratios are: bacteria, 23:1; actinomycetes, 7:1; fungi, 12:1; protozoa, 2:1; and algae, 0.2:1. Similar ratios for some of the more specialized groups within the "total" bacteria include: ammonifiers, 125:1; gas-producing anaerobes, 13:1; anaerobes, 2:1; denitrifiers, 1260:1; aerobic cellulose decomposers, 7:1; anaerobic cellulose decomposers, 1:1; spore formers, 1:1; and "radiobacter types", 1700:1. In all of these ratios except those given as 1:1, the differences in number in the bulk soil and in the rhizosphere (root surface and soil very close to the roots) were significant at least at the 5% level.

The amount of cover of the root surface by bacteria also has been examined. For example, Rovira, Newman, Bowen, and Campbell (1974) report on the cover on 8 species of plants; they found that it varied from about

4.7 to 9.3% for these species. They also observed, in a more detailed analysis than was carried out on the other species, that for Plantago lanceolata and Lolium perenne, not only was the interspecific difference of bacterial root cover significant at the 5% level, but Lolium was determined to have more Gram-negative bacteria in its root community than did Plantago. Newman and Bowen (1974) also examined the amount of microbial cover of the surfaces of the roots of Lolium perenne, Plantago lanceolata, and Rumex acetosa and found that there was no difference between younger and older roots.

More recently, Polonenko and Mayfield (1979) have examined the number of microorganisms growing at root surfaces and in the soils at various distances from those surfaces. Through the use of incubation chambers which permitted the direct examination of the roots and adjacent soil, they obtained data which show that the number of bacteria is frequently not significantly larger on the surface of the roots than it is in the soil within 4 mm of the root surface (there were, however, instances in which root microbial communities were considerably more dense than those of the adjacent soil). Polonenko and Mayfield also were able to use their apparatus and technique to observe the patterns of colonization and colony growth of the microorganisms which produced the rhizosphere communities (these patterns were seen especially well with the bacteria). This appears to be a useful technique;

further application of it will be rewarding.

Sivasithomparam, Parker, and Edwards (1979) examined population sizes of microorganisms of the roots of seminal and nodal roots of young wheat plants. They first washed the soil-freed roots gently, and then more vigorously (the latter was to shake them for 20 min. with glass beads, a process which involved mechanical breakage of some of the cells of the root surface). They reported that seminal roots had significantly more bacteria, actinomycetes, and fungi than did nodal roots (they worked only with the parts of the roots proximal to the plant crown, as the more distal roots were inextricably tangled together). In cultures from the vigorously washed roots (which provided population estimates from what they called the root residue), bacteria and actinomycetes were more abundant than from seminal roots but fungi were not. On the surfaces of both kinds of roots, there was a decrease in numbers within all three of these biological groups as the roots became older. In all three groups, however there was an increase in number within the "residue" as the roots aged.

It is not possible within the constraints of this paper to survey in detail the large literature which considers the effects of environmental variables on qualitative and quantitative aspects of the microbiota of the rhizosphere and the bulk soil. A few examples, however will be given to provide something of the flavor

of this literature and something of an entree to it. (There will also be more discussion of these factors below, within the context of a survey of the effects which (non-pathogenic) microorganisms have on the plants with which they are associated.)

The nature of the soil base material controls many of its environmental factors. Filip (1978) examined the effects of adding clay to cultures of various fungi and found that as little as 0.5% of montmorillonite resulted in considerable increase in their growth rates. Increases of 90 and 235%, respectively, were seen in growth of the yeasts Saccharomyces cerevisiae and Candida utilis, and their RQ (amount of carbon dioxide released per unit oxygen used) also rose. Also, in Aspergillus niger, for example, the RQ rose from 0.87 to 1.40 as a result of the addition of 10 mg of montmorillonite per ml to the buffered culture solution. Fenchel and Jorgensen (1977) also report considerable increase in the growth of bacteria in cultures to which small particles of relatively inert chitin were added. Not only did Filip find a change in the metabolism and growth rates of the fungi with which he worked, but there was a change in the chemical processes effecting the qualitative make up of the medium. In those to which clay had been added, there was a development of a dark brown color which indicated the production of humic materials from the glucose, while the cultures without the clay had only a slight yellow

coloration. Marshall (1975) examined the affect of clay minerology on soil bacterial survival, and also has broadly considered the effects that surfaces or interfaces have on the physics, chemistry, and biology of systems (see Marshall, 1976 and 1979 - - especially the 1976 book if considerable detail is desired). In sum, it is clear that within liquid culture or within soil the amount (and kind) of clay (and other materials) has considerable effect on the activities and composition of the microbial communities.

Large numbers of papers in the literature are concerned with the effects of level or availability of water on the size and structure soil and rhizosphere microbial communities, and on the rate of microbial processes such as population growth and decomposition of organic materials. One of these is that of Lund and Goksoyr (1980) in which pulse wetting of soil is carried out and the growth of various of the soil microbial populations is followed. When direct observation of soil bacterial populations was used to follow their numbers in a soil which originally had been moderately dry, there was a 6 day period of log growth of these populations following wetting, and after that the growth rate more or less leveled off. However, if a different technique of bacterial population evaluation is used, that of plate counts, the initial growth did not last as long, but was much more rapid. Also then, after the 5th day, when the

logarithmic growth had come to an end, there was a subsequent continuous reduction in the population instead of the maintenance of a rather constant population. Fungi, by contrast had linear rate of hyphal increase for the first 7 to 8 days. It is clear that these groups, separated at least partially by the observation technique which was used, represent largely different components of the microbial populations of the soil and rhizosphere, and that each group has different responses to an increase in the availability of water.

In a study of the distribution of fungi, actinomycetes, and bacteria along the length of wheat roots, van Vuurde and Schippers (1980) observed peak numbers on those parts of the roots which were from 3 to 5 and from 7 to 8 or 9 days old. They also used stain to determine the relative number of root cells which were still alive (their nuclei were stainable) along the root axis. Putting their data together they concluded that there is more important organic material addition to the areas around the roots as a result of lysis of or damage to the root cells than comes from simple exudation. The concentration of the microorganisms around the 3 to 5 day segments of the roots was highly correlated with the death (and presumably of lysis) of cells of the epidermis and outer cortex in roots of that age. The high microbial populations accompanying the 7 to 8 or 9 day segments were correlated with the activities of the lateral roots as

they pushed their way outwards through the root tissues, apparently damaging them in the process. As can be appreciated, these conclusions reached by van Vuurde and Schippers are generally contrary to those of McDougall and Rovira (1970) which were discussed above. Unresolved conflicts of this kind are, of course, to be expected in a field which is as young as is this one. They frequently may turn out to reflect more of the multiplicity of processes which occur in these systems rather than major experimental or interpretive errors which have been committed by the scientists involved.

In work which leads to conclusions which have some relationships to those of Lund and Goksoyr which were outlined above, Herzberg, Klein, and Coleman (1978) examined the population growth kinetics of Pseudomonas capacia and Arthrobacter sp. in continuous culture systems. These two bacteria, respectively, were chosen to represent the so-called zymogenous and autochthonous groups of soil and rhizosphere. The Pseudomonas had population densities which were 3 times that of the Arthrobacter at the lowest (similar) dilution rate of the chemostat. Viable cell numbers were lower than number of cells observed by direct count for both species, but the numerical relationship between them was pretty much the same. Total (dry) cell weight (which is a good measure of productivity of the species) was proportionally much higher, however, for the Pseudomonas (about 10X what it

was for Arthrobacter). As dilution rate of the chemostat was increased, there was relatively little effect on the above parameters for the Arthrobacter population, but a considerable decline in total cell number, and especially in cell dry weight for the Pseudomonas. There was also, after little change following modest increase in dilution rate, a considerable fall off in number of viable cells (and proportion of total cells which were viable) with its further increase. At the same time, with respect to energy charge of the bacterial populations, while there was little change in Arthrobacter, that of Pseudomonas increased considerably, from that which may have been the lower at low dilution rates through moderate levels at moderate dilution rates to appreciably higher for most of the higher dilution rates.

Response of the two bacteria to starvation was also quite different in that Pseudomonas rapidly lost its ability to respire while Arthrobacter did not; instead it kept its ability to respire and to utilize nutrients at low concentrations. Arthrobacter also showed an increase in ability to use some nutrients when nutrient level was low. The picture therefore provides a contrast between two normal rhizosphere bacterial species, Pseudomonas cepacia which is able to grow rapidly when nutrient levels are high, but which cannot maintain its population size under low nutrient conditions, and the Arthrobacter sp. which cannot grow nearly as rapidly, but which is much

more tolerant of the low nutrient levels which probably characterize most rhizosphere conditions most of the time. These Pseudomonas and Arthrobacter species therefore have many of the characteristics of r-adapted and k-adapted species, respectively (but one should not try to push this concept too far).

In a study which has some of the elements of that just discussed, Abdel-Nasser and Moawad (1975) observed increase in the populations of a number of groups of the rhizosphere microflora following the addition of a synthetic exudate (similar to that of wheat) to the soil. A number of bacteria (including Azotobacter, nitrogen fixing clostridia, denitrifiers, ammonifiers, aerobic and anaerobic decomposers of cellulose, and organic phosphate decomposers showed population increases, as did actinomycetes and fungi. Some species, including autotrophic nitrifying bacteria, however, had their populations depressed by this increase in the amount of rich nutrient material available.

Changes in the chemistry of the root exudates may occur very rapidly in response to the levels of environmental factors to which the plants are exposed. The related increase of photosynthate production with increased light levels and the resultant increased flow of photosynthate to Rhizobium containing root nodules on the roots of legumes (and the increase in nitrogen fixation rate which follows) is well known. By spraying urea or

benomyl on the aerial parts of wheat, Vransky, Stanek, and Vancura (1980) were able to affect the exudate produced by the roots and thereby affect the wheat's rhizosphere populations. For example, Pseudomonas fluorescens and Agrobacterium sp populations increased, as did those of amino acid requiring species in general, when urea was applied. On the contrary, when the systemic fungicide (benomyl) was sprayed on the wheat leaves, there was a moderate decrease in bacterial populations, and considerably more decrease in populations of the fungi. (The phytopathogenic fungus, Gaeumannomyces graminis var. tritici showed especially great decline under these conditions.) It is of particular interest that the fungi in general declined when urea was sprayed on the leaves. This appears to be the result of the additional available nitrogen leading to the production of more or better exudate, and the bacteria being able to take advantage of it more rapidly than the fungi and therefore being able to (somewhat) reduce the fungi by competitive pressures.

The study of Vransky, Stanek, and Vancura which was just discussed included observations relating to the effects which some of the microbial populations had on others in the rhizosphere. This topic will be considered at length below, from the point of view of the inhibitory effects of the normal rhizosphere/rhizoplane microbiota on the growth, survival and invasive ability of some of the obligate and facultative pathogenic species of

those plants.

A different kind of microbial interaction was observed by Ocampo, Barea, and Montoya (1975) when they inoculated Lavender plants (Lavandula spica) with Azotobacter and/or "phosphobacteria". After 16 weeks, populations of each species of the bacteria were larger in the presence of the other than when inoculated alone, and also the Lavender plants had greater weight when both bacteria were present. With the addition of manure, this pattern was maintained, and the bacterial populations and the plants all were larger. There were some problems with the paper, but the point made is certainly valid in general: there are many (and many kinds of) multi-species interactions of importance within the normal rhizosphere/rhizoplane of plants.

In one aspect of a long series of studies related to the interaction between soil organisms and the resultant rates of cycling of nutrients, Anderson et al (1978) found that the soil amoeba, Acanthamoeba polyphaga was able, in gnotobiotic culture where there were no other complicating biological interactions, to reduce the population of the soil bacterium, Pseudomonas cepacia. Also, the presence of the amoeba increased the level of the population of a soil nematode which feeds on both bacteria and amoebae. In a later continuation of this gnotobiotic work, Elliott et al (1980) report on a considerable interaction between the size of the particles of which the soil is composed

and the prey-predator dynamics of this bacterium-amoeba (and nematode) system. In a fine soil, the number of bacteria produced by a standard input of glucose was much smaller than it was in coarse soil (millions of bacteria per gram of dry soil on days 4, 14, and 33 were 7.6, 6.2, and 3.4, respectively, for the fine soil, and 68.2, 90.0, and 7.1 in the coarse soil (when no other species were present)). Addition of amoebae increased the number of bacteria in the soil early in the experiment, although it caused a depression of the bacterial number later on in the experiment in the coarse soil. These data, taken with other information given by Elliott et al illustrate considerable complexity of interaction between even a three species system, and point out how the nature of the soil may affect the interaction web. This should serve, in addition to its provision of interesting information, as a cautionary tale against too ready generalization about the dynamics of "the" microbiota-plant system.

Most plants have microbial species living with them which must be called mutualists because of the clarity of the benefit to both members of the pair of their living together. Mycorrhizal fungi and the plants that they live with provide one of the most widespread and common of examples. There are a number of fungi which live on or in plant roots which not only benefit the plant in the reduction of the possibility of attack of other species of microorganisms on the plant's roots (as will be discussed

at greater length below), but which also perform beneficial functions with respect to plant nutrition. The most striking (and probably important) of these is the increase in the amount of phosphorous made available to the plant through the activities of its mycorrhiza. Other nutrients also are made more available by mycorrhiza. For example, as reported by Daft (1979), inoculation of Rhizobium along with mycorrhiza resulted in increased availability of Ca, K, and P, in increased nitrogen fixation, and in larger and more diverse rhizosphere bacterial communities.

Finally in this section on the microbiota normal to roots and root-associated soil, a reminder is appropriate that the rhizosphere microbial populations present may have important effects on populations of different species which may be added. Pugashettk and Wagner (1980), for example, in work concerning Rhizobium japonicum strains (which cause nitrogen fixing nodules of Glycine (soybean) and Lupinus spp.) observed that in plant-free, sterile soil there was an increase in the Rhizobium population for four weeks following inoculation, then there was a two week population decline, and after that the population became stable. In non-sterile soil, by contrast, initially there was a decline which, although slow, lasted for about two weeks, and after that population numbers became stable.

As an addendum to this section, recent useful classifications of the root-rhizosphere region should be outlined: Old and Nicolson (1978), in considering what they call the microbial continuum of roots, distinguished four zones of that continuum (from outwards in): 1. rhizosphere, 2. hyphasphere (for the majority of plants which have mycorrhizae), 3. rhizoplane, and 4. root epidermis and cortex. Foster and Rovira (1978), with the aid of beautiful and detailed electron micrographs of roots and their surroundings, suggested a somewhat more detailed classification of the rhizosphere (from inwards out) and gave estimates of the approximate number of morphological types and number of cells of each which occur in each zone: 1. rhizoplane: 11;120 (these numbers refer to the number of morphological types separable on the electron micrographs, and the total number of billions of cells per cc of soil (not belonging to the plant) found in that zone), 2a. inner inner rhizosphere (0-5 micrometers from the rhizoplane, the surface of the root): 12;96, 2b. outer inner rhizosphere (5-10): 5;41, 3a. inner outer rhizosphere (10-15): 2;34, and 3b. outer outer rhizosphere (15-20): 2;3.

Microbiota of aerial plant parts.

Knowledge of the systematics, physiology, and ecology of the microorganisms which normally live on the above ground surfaces of plants also is poorly developed

compared to what we can see there is to be known.

Sampling from these aerial surfaces usually involves washing, and culturing of the washings, but Langvad (1980) recently has had some success in the examination of leaf fungal flora after removing it from its native surface with adhesives. Through simply sticking double sided scotch tape to microscope slides and then to the leaf, he has been able to look at distribution and number of the fungi. Thin layers of agar on slides also can be used, and they can be effectively incubated in moist chambers after the samples have been collected. Nevertheless this technique also is selective as some species will be much more easily removed from the leaf surfaces than will others -- and the problem of selective culturing still remains unless it is possible to identify all of the adhering individuals directly.

Plant produced organic substances are the major nutrient resources of the microbiota living on the aerial surfaces of plants. The reader will recall that substantial quantities of various carbohydrates and amino acids, not to mention some growth stimulating and inhibiting substances make their way to the plant surfaces (especially when those surfaces are wet), and from there may be washed off of the plant or may serve to support the microbial community on the surfaces. As Preece (1976) and Godfrey (1976) both pointed out, the kind(s) of plant-microbe interactions which occur are greatly

determined by the nature of these plant-produced chemicals. Godfrey comments on the relatively large amounts of organic materials lost to the leaf surfaces (especially of carbohydrates and amino acids), and in addition to considering these carbohydrates and amino acids, points out that a large variety of other kinds of substances are found there. These include phenolic compounds, 3-hydroxytyramine, gallic acid, gibberellic acid, abscisic acid-like substances, and others. One especially nice example of some of the kinds of dynamics which occur is that given by Preece (and mentioned above), in which the difference in leaf surface buildup time of plant produced nutrients (carbohydrates and amino acids) and of microbial inhibitors (phenols and others) is such that microbial community development can take place unimpeded for the first 5 to 7 days following leaching of the leaf surfaces. Only after that period is there replacement of the fungal inhibitors which also were washed away by the leaching. This is one reason that rain is frequently observed to be followed by an increase in plant disease incidence.

In a study concerned with the relative degree to which pathogenic and non-pathogenic bacteria adhere to leaves through mechanisms such as adhesive production, and of the degree to which any such adhesion may relate to adaptation to the host by the pathogen or to stimulation of the bacterium by its host (to produce (more) adhesive),

Leben and Whitmoyer (1979) examined the rate at which various bacteria were washed off of host and non-host leaves. After cell suspensions of the various kinds of bacteria had been in contact with the leaf surfaces for 10 min., a standard water stream was found to wash them off at a straight line, log-log rate. This was true for Pseudomonas lachrymans on both its host, cucumber, and on non-host chrysanthemum. Non-pathogenic species tested (Escherichia coli and Serratia marcescens) also showed the same pattern. The conclusion to be drawn from these data is (at least within this rather considerably limited sample) that adhesion to the leaves is non-selective, and not related to particularly well developed specific host-pathogen interaction.

It is clear from the studies of Langvad and of Davenport (1976a) among many others, that there is considerable spatial, temporal, numeric, and species variation in the above ground plant surface microflora. Davenport also points out that animals may have important effects on these distributions by transporting the microorganisms or by providing nutrients for them (feces, honey dew, and so on).

Billing (1976), in a discussion of the systematics of the bacteria of the surfaces of the aerial parts of plants, lists the more common species as belonging to the genera Erwinia, Pseudomonas, Xanthomonas, and Corynebacterium, with less common but frequent inhabitants

belonging to Bacillus, Lactobacillus and, faecal streptococci (enterococci). She goes on to point out that "Bacteria associated with plants can no longer be considered a class apart; many, though distinctive, have affinities with bacteria from other habitats including humans and other animals, soil, water and foods". On the other hand she points out that our "knowledge of the characteristics of bacteria on plant surfaces, apart from pathogens, is still scarce...". She and others have also emphasized the spatial and temporal variability of the communities (and the species making them up) on aerial plant surfaces.

In another paper, Davenport (1976b) discusses some of the great effects which choice of technique may have on the completeness and validity of studies of the species composition and/or the numerical relationships among species of aerial plant surfaces. He uses agar culture plates (with their recognized problems) and concentrated on two factors: the method of sampling of the surfaces, and the incubation conditions. Estimates of population sizes of the communities of dormant buds, leaf blades, petiole bases, and immature fruit of grape increased by a factor of about 3 to about 1700 as surface washing was replaced by maceration of the plant tissue (there obviously was the addition of material from the plant on which the organisms had been living in the maceration part of the experiment, and this may have been the cause of

some of the increase in the estimates of those population sizes). In other experiments, Davenport compared the sizes of the populations which he could obtain on agar surfaces after incubation at 5°C with those obtained at 25°. There were 7 times more colonies which developed at the lower of these two temperatures, and in addition, there were 15 spp. of yeast seen at 5° and none at 25. The high temperature is modest compared with what the upper surfaces of leaves achieve when the sun shines on them, nevertheless it should be kept in mind that most of the time when the leaf surface is wet (as the agar surface was in some degree), leaf surface temperatures usually are lower than this from rain cooling, cool fronts, etc.).

In a study of the microbiota of olive (Olea europaea) leaf surfaces, Ercolani (1978) found that the sometimes pathogenic Pseudomonas savastanoi (it is the causal organism of olive knot disease, which sometimes can be serious) comprises a highly dominant fraction of the total leaf microbiota. It makes up as much as 68% of the individuals on olive leaves, and the next most common species, Erwinia herbicola, accounts for only about 8%. There are also another 10 or so spp. which usually make up about 1% each of the population on the average. One must keep in mind that these data, too, suffer the possible problems related to the use of agar plate techniques. It is of considerable interest that this well known pathogen of olive is so dominant on leaves of

healthy trees. Apparently it is only able to enter the tissues of the plant when there has been some damage to the plants mechanical defenses; the most common cause of such damage is the wounding of the young stems which occurs as a result of freezing. Pseudomonas savastanoi also attacks other plants, Fraxinus (ash), Nerium (oleander), and Ligustrum (privet), and this suggests (along with the fact that it needs wounds to be produced before it can attack the olive) that it is not a well co-evolved parasite of its host. It may be in the process of developing the parasitic habit after having been a leaf saprophyte.

In an examination of one of the environmental factors which may be important in the determination of the structure of aerial plant surface microbial communities, Szejnberg and Blakeman (1973) observed the effects of ultraviolet radiation on some of the biota of leaves. They used 50 or 2000 microwatts per square cm, from a source which had peak output at 253.7 nm. They observed no consistent decrease in the bacterial populations of dry leaf surfaces, but in populations on leaves which were and had been wet there was rapid mortality. There was another interesting effect of the UV, that of stimulating increased leakage of both carbohydrates and amino acids from the leaves. These additional nutrients on the leaf surfaces resulted in increased germination of the spores of (the pathogenic fungus) Botrytis cinerea. This

germination increase, however, did not last long - - it fell off after about 48 to 72 hrs. Apparently what happened was that the spores were able to germinate well when bacterial populations were relatively low, but with time these populations achieved adequate numerical response, and grew to the point that they inhibited further Botrytis germination by reduction of nutrient levels and/or by antagonistic interactions with the fungal spores.

As outlined above for some of the bacteria, some of the pathogenic fungi also live on aerial plant surfaces for extended periods without attacking the plant. Dickinson (1976) discusses the ability of many fungi which normally are surface inhabitants of leaves of green plants to sometimes invade those plants and live as parasites. Genera of fungi known to have this ability are: Alternaria, Aureobasidium, Fusarium, Phoma, and Stemphylium. He also points out that a number of species generally considered to be normal pathogens nevertheless have extensive spatial and/or temporal non-parasitic growth phases on plant surfaces prior to invasion. Dickinson goes on to indicate that presence of pollen grains or of honey dew on the leaves may have considerable effect in the stimulation of fungal populations.

Warren (1976) supports Dickinson's claim of a large effect of pollen. He dusted uncontaminated Agrostis pollen on birch and on basswood leaves and found increases

of number of fungi per gram leaf (as compared with pollen-free leaves) of 5,100 to 260,000 for Betula, and 100,000 to 430,000 for Tilia. He goes on to indicate that in some species of trees, fungi (and bacteria) cannot get inside the bud scales, but that in others the inner furled leaves of the bud, and even its apex may be colonized.

One of many possible examples of work on the effects of plant or leaf age on the development of a microbial community is discussed by Collins (1976). He attempted to standardize his experimental procedure by using leaves of Antirrhinum (Snapdragon) which he detached from the plant and kept under controlled conditions. In sporefall of Sporobolomyces roseus, he found that old leaves captured many more spores than did young leaves, and that there also were greater amounts of both carbohydrate and amino acids in leachates from older than from younger leaves. He observed an antagonism between Sporobolomyces roseus and Cladosporium cladosporioides, and generalized to say: "Microbial populations on leaves could also be restricted by mutual antagonism between phylloplane saprophytes."

After measuring the amino acids and the carbohydrates found in water droplets collected from the leaves of lettuce and watermelon (watermelon produced, by this measure, something over 3 times as much of each as did lettuce), Chet, Zilberstein, and Henis (1973) made up various artificial mixes and tested the response of Pseudomonas lachrymans to them. They found that this

bacterium has a chemotaxis which causes it to respond better to a mix of sugar and amino acid than to either one of them alone.

Biological Pathogen Control.

In addition to the mechanisms by which plants themselves make invasion of their tissues difficult for microbial species (a variety of which were discussed above), there is an important group of processes by which plants are, in effect, aided by a number of microbial species in their avoidance of attack by other microbes which may harm them. As far as is now known, the first paper which had to do with this kind of effect was that of Le Berryais (1785) in which it was reported that microbial invasion of pruning wounds was reduced by the application of wet mud to the wound. Le Berryais, of course, did not understand what the helpful mechanisms was; much later, Grosclaude (1970) repeated the experiment with the same result. He was able to reduce the rate of infection by Stereum purpureum from 100 to 30% by coating the wounds with fresh mud the day before inoculation with the pathogen.

The first experimental demonstration of direct and plant protecting interactions between the microbiota normally associated with the roots of plants and pathogens capable of attacking the plants apparently was provided by Henry (1932), who found that wheat seedlings were attacked much more readily by Ophiobolus graminis (now known as

Gaeumannomyces graminis var. tritici) when they were in otherwise sterile soil than when the soil contained the normal rhizosphere microbial community. This attack on the wheat by the pathogen was not successful at temperatures which were relatively unfavorable to the pathogen, but on the other hand, at the optimal temperature for the pathogen, there was little protective effect of the normal rhizosphere flora. The dependence of the effectiveness of biological control on the level of non-biological environmental factors (of which this is only one of many possible examples), is one of the reasons that it has taken as long as it has to recognize and utilize some of the biological control mechanisms.

Since the time of Henry, however, there has been a growing interest in and work on these problems. The most complete summary of this kind of work which has been written to this time is the book which Baker and Cook published in 1974. In this they provide an excellent survey of biological control of pathogens within the broad context of consideration of the ecology of pathogen-host relationships. This book is to be highly recommended.

The plan of the remainder of this section will be first to examine a number of the experiments which illustrate that there is at least some influence (and sometimes very great influence) of the normal plant-associated microbiota in the reduction of the probability of successful pathogen attack on the plant.

This discussion will be developed within the context of a recognition of the spectrum of degree to which microorganisms are adapted to the parasitic habit, and to the ecology of the various species as this is related to the closeness of this adaptation. As was pointed out above, parasitism may vary from that in which a microbial species can successfully attack a plant only under unusual (and rare - - and perhaps extreme) conditions, in which everything must be "just right" to that in which the pathogen is very highly adapted to the parasitic habit and can almost always be successful in an attack on its host after it reaches the host's surface. In the former kinds of pathogens, the variety of plant species which may be attacked by the "pathogen" usually is quite great, in the latter, where the pathogen is highly specialized, it frequently is restricted to a single plant species, and sometimes to only one or a few varieties or strains of that species.

Plant pathologists (Baker and Cook, 1974; Agrios, 1978) have categorized these two groups of pathogens: Non-obligate pathogens, which tend to have wide host ranges, may attack a number of the different kinds (or ages) of the plant's tissues, and frequently have considerable populations which live saprophytically for extended periods of time on or near potential hosts. Obligate pathogens, by contrast, have restricted host ranges, frequently are restricted to particular tissues

within a host which they attack, and are generally much less able to exist as saprophytic populations. Frequently the non-obligate parasite requires the organic exudates of the host to maintain its populations (and perhaps to provide for their growth) at levels and sites which permit the eventual invasion of the host. Obligate parasites, on the other hand, have relatively little requirement for host exudates, and when they can reach the host they are generally effective in its invasion. In addition, the non-obligate pathogen is most effective and successful in its attack on potential hosts when those hosts are in poor or weakened condition as a result of unfavorable environmental factor levels, while the well adapted pathogen frequently does best when the levels of environmental factors are especially favorable to the well-being of its host.

Clearly there is a multidimensional axis from the most highly adapted pathogenic species to those which are non-obligate (and perhaps almost could be called casual). Microorganisms which can attack plants are scattered along this axis, and a number of them will have characteristics which are somewhat intermediate of those which have been used to categorize those at the ends of the scale.

In any event, there are two general kinds of effects which the non-pathogenic microbial communities can have on (potentially) parasitic species. One of these is the simple competition for nutrients or for space, what

ecologists would call exploitive competition, in which the species which was able to first and/or more efficiently appropriate the resource to its use would win. The other kind of competition, interference competition, is where one species affects the other in a negative fashion through its behavior and/or the chemicals which it releases. In addition, as mechanisms which affect the probability of a microbial species being able to successfully attack a plant, hyper-parasitism on the potential parasite, or the activities of another species which eats it, also can be important.

It is clear that those well adapted pathogens which do not require organic nutrients from their hosts will be little affected by competition by the normal saprophytic microbiota of a plant (although in some instances, such as where the saprophyte has covered the surfaces of the potential host, the mechanical barrier which is presented may be important). For these well adapted pathogenic species, therefore, only the mechanisms of interference competition, and of hyper-parasitism and predation on them will be effective. For the pathogens towards the non-obligate end of the axis, on the other hand, all of the mechanisms outlined may be effective.

In addition to the early results which were outlined in the beginning of this section, in which the normal microbiota of plants was shown to protect them from pathogen attack, Muller-Kogler (1938) observed that the

take-all fungus Gaeumannomyces graminis (which at that time was called Ophiobolus graminis), which normally attacks only grasses, will cause at least slight infection of the root cortex of at least 73 species of dicots when they have been deprived of their normal microbiota. Eaton and Rigler (1946) observed that corn roots were attacked by Phymatotrichum omnivorum when they were grown in sterile soil, but not when they were grown in non-treated field soil. This root rot fungus grew under both conditions, but did not cause lesions on the roots and result in plant death unless the normal microbiota was absent. Lettuce was protected from attack by Botrytis cinerea under the right conditions by Pseudomonas sp., Bacillus sp., and even by Escherichia coli. In the latter two, temperatures of from 15 to 20° C were required for inhibition of the fungus, but Pseudomonas also was effective at 4° (Newhook, 1951a and b). These different patterns of response with different temperatures make sense in the context of the requirement of B. cinerea for low temperatures for its best growth, and its relative intolerance of temperatures above 21°. This experiment of Newhook was especially nice because of its "successful" use of E. coli, which certainly cannot be called one of the normal members of the leaf flora (although Billing, 1976, pointed that members of the enterobacteraceae (including E. coli) are not rare on leaf surfaces).

The most simple mechanism by which some of the normal microorganisms of plant surfaces may protect the plants with which they are associated from pathogens is the provision of a physical barrier which keeps the pathogen from the plant. Marx (1972), for example, points out that ectomycorrhizae, although they may also produce antibiotics and have other mechanisms which operate to the detriment of pathogens, frequently cover plant roots with dense layers of hyphae. These layers are also frequently multiple, and because of their thickness, density and structure, appear to provide a physical barrier of some importance.

In more recent work there has been more attention to the separation of saprophytic competition from antagonism through (primarily) the production of antibiotics. As was suggested above, the fact that plants normally release appreciable (and sometimes considerable) quantities of organic materials, including compounds which contain elements which may be in somewhat short supply to the plant, is strong evidence of the usefulness of the normal microbiota to the plant. It is clear from the current literature that this microbiota carries out a number of activities which are in one way or another helpful to the plant (in addition to the antipathogen activities discussed here).

Crosse (1971) reminds us that upon occasion, species which normally are non-pathogenic (and which may provide

the plant with protection from pathogens) accompany the pathogen into the plant when invasion is successful. Erwinia herbicola, for example, may be what is called a secondary invader of diseased plant tissue, and it and other secondary invaders may either cause an increase or a decrease in the amount of damage done to the plant by the primary pathogen.

The evidence is that at least some of the pathogen inhibition mechanism by which the normal leaf microbiota decreases Botrytis cinerea or Mycosphaerella ligulicola attack on leaves is the result of competition for the dissolved organic material on the leaf surfaces. Fraser (1971), for example, has demonstrated this experimentally when he was able to reduce the rate of attack of B. cinerea by application of any of 5 species of bacteria to the leaf surface. However, Botrytis inhibition did not occur when he also put additional organic resources on the leaf (he used 1% dextrose or pollen grains). When the spores of either of the two fungi were trapped in small water droplets on the leaves, the bacterial populations in those droplets increased much more than in sporeless droplets. It is clear that the spores lose organic materials which the bacteria can take up (and it has been suggested elsewhere, that if bacteria do not rapidly remove the organic materials leached from spores, the germinating spores will be able to reabsorb and use them). Blakeman (1972) also worked with this system, and found

that of 9 bacterial species examined, all inhibited the growth of B. cinerea, and that a pale yellow Pseudomonas which had voluntarily colonized the leaf surfaces (and apparently entered somewhat into the leaf tissues) was the most effective. This inhibition, however was observed on leaves of beetroot (Betula vulgaris) plants which were 9 weeks old or older, but not on leaves of 6 week plants. Blakeman observed an increase in the amount of amino acids which were found in water droplets on the leaves as the plants became older, and suggests that higher bacterial populations which developed on the older leaves were in response to these amino acids, and that the increased level of inhibition of the mold was a result of those higher bacterial populations. Brodie and Blakeman (1975) worked with this same system in vitro. They found that Pseudomonas took up the lion's share (about 80%) of the amino acid glutamine which had been added at levels comparable to those found (for total amino acids) in water droplets on beetroot leaves. B. cinerea conidia took up less than 10% of the glutamine; some of the difference between amounts taken up by the two species was the result of much more rapid uptake rates (when measured in single species cultures) by Pseudomonas than by Botrytis conidia.

It might be well, at this point to remember the report of Preece (1976) in which more rapid return to pre-washing values occurred for carbohydrates than for plant produced pathogen growth inhibiting compounds on the

leaves of plants. Purnell (1971) made this same point earlier, although he observed a slower buildup of fungal inhibitors (which took about 12 days).

In a study of interactions of phylloplane bacteria with Botrytis squamosa and B. cinerea on onions, Clark and Lorbeer (1977) found that of isolates of 13 species, only 2 inhibited the molds (the number of lesions produced was the measure). On the other hand, 10 of the bacterial species caused an increase in the number of lesions which developed on the leaves. The fungal flora of the (outdoor) onion leaves had a weak inhibitory effect (at the level of 10 to 5000 removable fungal propagules per sq. centimeter). Clark and Lorbeer agree that the mechanism of the bacterial inhibition probably in that of reduction of nutrient level on the leaf to the point that the spores of the molds germinated less well.

In other work with onions, Coley-Smith (1976) observed that the microbial populations of the normal soil inhibited the germination of the sclerotia of Sclerotinium cepivorum (the cause of white rot in Allium). It was only when exudates of the normal host appeared that this inhibition was overcome and the sclerotia germinated. He comments that this highly host-specific germination response "is unusual or perhaps unique amongst plant-pathogenic fungi". A similar, although less striking condition exists between Stromatinia gladioli and its hosts: germination of the sclerotia was from 0 to 73%

(with a median of 28%) for 16 species or strains of the Iridaceae, but with 8 other plant species, each a member of a different family, germination rates were from 1 to 3%. Coley-Smith points out that sclerotia leak nutrients when they are wet, and agrees with the general consensus in the literature that when bacterial populations are sufficient, the leaked products are utilized rapidly and therefore are no longer available to the germinating sclerotia. Leakage rates vary considerably among the fungi, and S. cepivorum and its relative S. oryzae either lose the most or are more sensitive to a given loss than are most. Similar leakage patterns and dynamics have been suggested for conidia.

The number of microorganisms coating the surface of a root is dependent on the plant's environmental conditions. Schippers and van Vuurde (1977) found considerable increase in the number of organisms (and presumably a comparable increase in the effectiveness of any physical barrier which they provide for pathogens) as the result of spraying wheat leaves with a dilute urea solution. The number of organisms which displayed antagonism to wheat take-all (G. graminis) also increased. Some of the more normal environmental variables probably have as great an influence on the degree to which the plant associated microbiota protects it against pathogens.

Disease incidence can be considerably reduced (or increased) by amendment of appropriate materials into the

soil. For example, growing and plowing in a cover crop of barley results in decrease of bean root rot (caused by Fusarium solani f. sp. phaseoli). Baker and Cook (1974) cite their own work which shows the mechanism of this reduction of bean root rot to be that the straw which was incorporated into the soil was so nitrogen poor that competition for nitrogen was severe; Fusarium solani cannot withstand this and as a result starves. Other high carbohydrate, low nitrogen materials (sawdust, cellulose, sugar, and so on) have similar effects. As we shall see below, soil amendment can also result in an increase of species which produce anti-pathogen antibiotics or which attack the pathogen directly and destroy it. Which populations are stimulated to grow (and therefore which mechanism(s) may be brought into action) depends in some measure on the nature of the amendment. Experimentation with soil amendment continues, with Guy and Baker (1977), and Dutta and Isaac (1979), as examples, adding cellulose, green manure, and chitin. Guy and Baker found chitin to reduce Fusarium wilt in peas, and Dutta and Isaac saw reduction in attack of Verticillium dahliae on Antirrhinum (snapdragon) with amendment by chitin or green manure. Cellulose addition, on the contrary, increased the attack rate on the snapdragons.

Black (1968) was one of many who observed strong interaction between soil microflora and pathogens. He reported that in sterile soil, Phymatotrichum omnivorum

was able to penetrate into the cortex of corn roots, while in the presence of the normal microflora, the mycelia of the pathogen were able to develop, but could not get close to the roots. He postulated interference by the rhizoplane microbiota, and the pattern certainly looks as if it is one which is caused by anti-Phymatotrichum materials which were produced at or near the root surface by these microorganisms. Inhibition by antibiotics apparently was the cause of the reduction by Aureobasidium pullulans of attack on bean leaves by Alternaria zinniae as reported by Van den Heuvel (1970). He had isolated the Aureobasidium from bean leaves, and found that the greater the interval of its inoculation onto leaves before the Alternaria was added, the greater the protection which was provided. As with a number of workers, Van den Heuvel looked to the host's surfaces for species which might be effective in protecting it from its pathogens.

Rai and Saxena (1975), exemplify a useful variation on the above theme (which also is used frequently), when they isolated sclerotia of the destructive pathogen, Sclerotinia sclerotinorum and then isolated other species from the surface of these sclerotia. The reasoning is that the species which can be "caught in the act" of sticking to the surface of a pathogen life cycle stage very well may be there because it is attacking that pathogen. Of the 24 other fungi which Rai and Saxena obtained in this way, 9 demonstrated in vitro antagonism

against Sclerotinia sclerotinorum (Penicillium spp. were especially important). In addition, some of the other species which were not effective in vitro, were antagonists to S. sclerotinorum when they were added to pathogen infested soil.

Both uredospore germination and their subsequent production by Puccinia graminis tritici on wheat leaves were inhibited by a number of fungi which were isolated from the wheat phylloplane. Wheat rust germination was inhibited by more of the species (18 spp.) tested than was the reduction of the production of the uredosori (9 spp.), according to Mishra and Tewari (1976).

Cook and Rovira (1976) outline the very interesting story concerning the development of "suppressive" soils in grain fields after the field had been planted in wheat continuously for a number of years (see also Baker and Cook, 1974). Wheat take-all (Gaeumannomyces graminis var. tritici) is one of the most serious pathogens of wheat, and it turns out in a few soils when they are first plowed, and in others after they have been continuously planted in wheat for a number of years, that the take-all fungus is relatively ineffective in its attack on the wheat. In addition, in some instances, when continuous planting of wheat was interrupted for a year or two by crop rotation, attack of take-all on the first few crops planted thereafter was greater than it had been before the rotation. In a few years, however, the suppressive

quality returns to the soil if wheat is planted year after year. The antagonism to take-all turned out to be transmissible from one soil to another by use of relatively small inocula of the suppressive soils. Cook and Rovira (1976) suggested that the suppressive agent is the common soil bacterium Pseudomonas fluorescens (and that only some strains may be effective). What happened, they believe, is that the bacterium is found in relatively high numbers in some soils (the naturally suppressive soils), that in some soils it may grow from originally small populations to much larger ones if wheat is planted year after year (and in becoming larger makes those soils suppressive), and that soils bearing it can be used to start populations in other soils which originally do not contain it. This is a beautiful example of how important it is not to generalize too quickly - - for example it is well known that by far one of the most effective methods of control of many plant pathogens is to provide for appropriate crop rotation. In the particular case of take-all and wheat, however, it can be seen that this is the very worst thing to do, as it results in the rapid decline of the fluorescent pseudomonad which attacks the take-all fungus and the rapid reduction of the suppressive characteristics of the soil.

Phytopathogen populations, of course, also may evolve mechanisms which will tend to counter the activities of some of the other species of microorganisms which act

against them in one way or another. For example, fungi which have sclerotia which lose leaked nutrients to nearby competitors, or which may be affected by antibiotics of their neighbors, may develop antibiotics of their own. As one instance of where this has happened, Coley-Smith (1976) reports that some species of fungi have developed the ability to release antibiotics (ergot is one of these) along with the other leakage of organic material which they seem unable to avoid when they become wet. It seems reasonable that these antibiotics may well have inhibitory effects on individuals of other species which otherwise would take up much of the leaked organic product with the result that the fungus would not have it available for readsorption.

An example of how misleading experiments on agar can be is to be found in the paper of van der Hoeven, Mitali, and Gindrat (1979). They found 39 isolates from places which had good probability of harboring antagonists of the cucumber black rot organism, Phomopsis sclerotioides, to be effective antagonists of that fungus on agar. However, only 4 of these showed promise of controlling the fungus when tested in the context of cucumber seedlings growing on blotting paper. It may very well be, in addition, that in the context of the soil and the normal microbiota found there, the list of effective Phomopsis antagonists will be different from that determined by either of these tests.

In the continuing development of our understanding of the interaction of the take-all fungus of wheat (Gaeumannomyces graminis var. tritici) and Pseudomonas fluorescens (and sometimes P. putida), Smiley (1979) reports on the effect of soil and rhizoplane pH on the results of the dynamics. Populations of take-all are lower (in non-alkaline soils) when ammonium instead of nitrate is used as the nitrogen fertilizer. This is because rhizoplane pH is lowered when the roots take up ammonium (by up to 2.2 pH units in the greenhouse, and 1.2 pH units in the field) with the result that Gaeumannomyces growth is greatly inhibited. (Take-all fungus grows poorly if at all at a pH of less than 5.0, and in some soils at a pH of 5.0 to 6.5.) Because of this, the pseudomonads, which are more tolerant of the lower pH, can be especially effective under these conditions.

Wong also has worked with the take-all fungus, and reports (1980) that temperature affects the interaction between it and some other fungal species which under some conditions are antagonists. He found that of 4 fungi which would protect wheat against the pathogen at the relatively high temperatures of the lab, only those which were capable of growing well at lower temperatures were able to provide protection in the field. This is because it is quite cool in S. Australia where he was working, and as a result some species which had shown considerable promise in the greenhouse did poorly in the field. This

kind of observation illustrates one of the many reasons that greenhouse experiments frequently do not translate to the field successfully.

Rai and Singh (1980) examined the activity of some of the normal phylloplane fungi in protecting mustard from Alternaria brassicae (causal of "leaf spot"), and in protecting barley from Drechslera graminea. They did most of their work in the field and found that 11 fungi protected these plants from their pathogens in some degree. One point which is of special interest is that the same fungi were effective in inhibition of different pathogens on different hosts. They observed that a mixture of all 11 of the pathogen antagonists was almost always more effective than any one of these species alone, that the temporal relationship between inoculation with the pathogen and with the antagonist was important (earlier antagonist inoculation was better and later was worse), and that in many instances antagonist culture filtrate was of considerable effect in the inhibition of the pathogen. They also found, to no surprise, that the pattern of interaction in the field was different from that which was seen on agar.

Damping off in sugar beets which is caused by the fungi Aphanomyces laevis, Pythium ultimum, or P. debaryanum may, according to Vesely (1978) be preventable by inoculation with P. oligandrum. Not only is P. oligandrum a hyperparasite on these other fungi, but the

plants had greater weight when it was present (in sterile and non-sterile soils and regardless of the presence or absence of these pathogenic fungi).

Utkhede and Rahe (1980) used a wet-sieve flotation isolation technique to concentrate sclerotia of the white rot onion pathogen, Sclerotium cepivorum. From these sclerotia, they obtained 4 isolates of Bacillus subtilis and one of Penicillium nigricans which produced effective antipathogen antibiotics on agar. Upon testing these in the field, the bacillus gave season long protection to onion cultivars which were partially resistant to white rot, and gave partial (but significant) protection to a fully susceptible cultivar. The Penicillium, on the other hand, while it helped a little, did not provide protection which was very long lasting.

In work with the 4 most damaging fungal pathogens of conifer root systems in the western United States, Hutchins (1980) found a Bacillus sp., which is fairly closely related to B. cereus and which (at least on agar) effectively inhibits all of the 4 fungal pathogens (Phellinus weirii, Armillariella mella, Fomes annosus, and Phytophthora cinnamomi). Only time and further experimentation will tell if these interactions also will work in the forest.

In a somewhat different vein, Anderson et al (1980) were able to isolate a bacterium from the caryopses of

Tripsacum dactyloides which greatly inhibited the growth of Penicillium chrysogenum, Rhizopus stolonifera, and Trichoderma viride (but not of Alternaria sp. or Fusarium moniliforme). They speculate that this bacterium (Pseudomonas sp.) may be important in the prevention of attack on the caryopses of Tripsacum by soil fungi during the many months that they may lie in the soil before germinating.

A large number of environmental factors can variously affect, depending on their levels, the interactions which occur between plant pathogens and the non-pathogenic microorganisms of rhizosphere or phylloplane. For example, earlier it was pointed out that the addition of pollen to leaf surfaces may have considerable effect in increasing the level of pathogen attack on that leaf. Fokkema (1971) observed significantly higher germination rates of the spores of the rye pathogen, Helminthosporium sativum, and much higher mycelial length and number and density of lesions which it caused on leaves which had pollen on them than on leaves without pollen. On the other hand, Warren (1972) reported that infection of Beta vulgaris leaves by the fungus Phoma betae occurred on 88% of the leaves without pollen and decreased dramatically to only about 3 to 5% on leaves which had pollen on their surfaces. It would appear that in one instance the organic materials which leached from the pollen grains were much more of a stimulus to the pathogen and that in

the other these pollen-derived compounds either inhibited the pathogen or provided nutrients for the growth of non-pathogenic phylloplane species which inhibited the pathogen either by competition (the less likely under these conditions?) or by the production of antibiotics.

After pointing out that pathogens which can only attack young or juvenile tissues will continue to be dangerous to the plant because it must continue to produce roots (with their juvenile tissue), Garrett (1979) goes on to discuss suppressive soils. He reviews the situation of take-all and cereals, and also considers the interaction of Fusarium oxysporum f. sp. cubense (the "Panama disease") and bananas. In some soils, even though the pathogen is present, it is not a very serious problem. This condition seems to be related to the presence of a sufficient proportion of montmorillonite clay which appears to make the soil more favorable for one or more bacterial species which in turn inhibits the pathogen. (Recall Filip's results (1978) in which he observed considerable change in growth rate and physiology of various fungi on the addition of montmorillonite to their culture.)

In experiments on the parasitism of the plant pathogen, Rhizoctonia solani by 3 different species of Fusarium, Arora and Dwivedi (1980) observed frequent attack of Fusarium on Rhizoctonia in which hyphae of the former coiled around and/or penetrated destructively into

hyphae of the latter. Their work was done on staled agar, and in some instances there seemed to be a reversal of the normal effect of an attack (when F. udum hyphae were seen to undergo lysis within R. solani hyphae). The cautions suggested above about the problems of whether or not the same kinds of interactions occur in the field also need to be kept in mind.

Measures of the effects of predation of protozoa on normal plant microbial communities, and on the phytopathogens frequently associated with them are very few. Darbyshire and Greaves (1971) reported that damage to pea roots by a Pseudomonas sp. which they isolated from Timothy Grass rhizospheres, was not reduced (or increased) by the soil amoeba, Acanthamoeba palestinensis. The amoebae penetrated (as did the pseudomonads) many of the epidermal and outer cortical cells of the root, but their effects on the bacterial population were not adequate to change the amount of damage that the bacteria did to the roots. Darbyshire and Greaves also observed that the pseudomonads invaded the pea roots only when the normal microbial community was absent (the soil had been sterilized by gamma rays); they did no observable damage when that community was present.

Although information on it has not yet been published concerning the situation when plants (roots) are present, the work of Elliott et al (1980) on a gnotobiotic soil system containing Pseudomonas cepacia, Acanthamoeba

polyphaga, and a nematode which can eat both is of interest. In this and in some of the other reports of Elliott and his colleagues, descriptions of very interesting dynamics involving various combinations of these species are given. For example, different population sizes of the various species were found when particle size of the soil was varied. In an earlier work, Elliott, Coleman, and Cole (1979) working with gnotobiotic systems containing Blue Grama grass (Bouteloua gracilis), Pseudomonas cepacia, and Acanthamoeba polyphaga in various combinations, observed very interesting different results of the different dynamics which occurred. For example, although plant yield was not affected (in a 60 day period) by the combination of soil organisms included, the nitrogen content of the grass tissue was appreciably higher in systems which contained both the bacterium and the amoeba than in those which had only the bacterium.

In summation of this section, and from the book of Baker and Cook (1974), and the review papers of Fokkema (1976), Blakeman and Brodie (1976), and Skidmore (1977), one can say that the normal microbial community on or very near to the surfaces of plants plays very important roles in the protection of those plants from pathogens. The mechanisms of this activity include: 1. reduction of levels of organic compounds on or near the plant surfaces (including reduction of those which leak out of pathogen dissemules), 2. production of antibiotics which inhibit

germination of pathogen spores and growth of pathogen hyphae or populations, 3. change of pH to levels which are less favorable to pathogens, 4. production of mechanical obstruction which keeps the pathogen from being able to attack the host, 5. stimulation of immune reactions of the plant (phytoalexin production), 6. hyper-parasitism on the pathogen, and 7. predation on the pathogen. No doubt there are others. It is also clear that the dynamics of the most simple of natural systems is of considerable complexity and that we have much to learn before we understand it well.

Non-protective direct microbial effects on plants.

Plant growth inhibition by non-pathogenic microbes

There is a scattering of reports in the literature of experiments in which it has been shown that various microorganisms or microbial communities can reduce the amount of growth that plants have (as compared to similar treatments from which microbes were excluded). One of the earlier of these studies was that of Bowen and Rovira (1961) in which plants (tomato, phalaris, radiata pine, and subterranean clover) were grown on sand and on agar, and inoculated with the microbial communities of 4 different soils. Primary root growth was reduced by the microbial communities for all of the plants, and total root length was reduced in most. The number of root hairs also was reduced (especially in the clover). There was, however, a tendency for an increased number of secondary roots in the non-sterile systems. However, the pine had greater growth of the tops in the microbe-containing systems, although none of the other species showed this effect.

Lynch and White (1977) found that mated cultures of Blakeslea trispora produced trisporic acid which inhibited both root and shoot extension of barley. It is most interesting that neither of the unmated strains either produced trisporic acid or inhibited root growth. Azotobacter chroococcum had variable effects on barley

growth, and was able to at least partly neutralize the inhibitory activities of (mated) B. trispora. Addition of sugar to the B. trispora/plant system resulted in an increase in its growth inhibitory effects. In addition, Lynch (1978) demonstrated that there may be an important effect of microbially produced acetic acid on rape, barley, wheat, clover, and maize when enough plant residue is combined with the soil. He used a "residue" of straw and found not only that acetic acid was produced by microbial activity at the straw surface, but also that as far as 1.5 cm from this residue the acetic acid concentration could be about 1/2 what it was at the straw surface (in non-calcareous soil). Exudation of carbohydrate by the seed which occurs normally, also may result in further increase in microbial activity and an increase in the amount of acetic acid produced. This may be especially dangerous as increased microbial activity also causes the oxygen concentration to fall, and the amount of exudate produced by the seed is increased by low oxygen levels. This in turn stimulates more oxygen consuming and acid producing activity of the bacteria, and a vicious cycle is set up which well may lead to the death of the seed. Acetic acid production is seldom a problem in calcareous soils, and it may be mitigated elsewhere by coating the seeds with a CaCO_3 layer. (It is the acetic acid more than the pH which causes the problem -- the acid in the undissociated state appears to be especially toxic, perhaps, Lynch suggests, because it can then

penetrate the lipid components of the cell membrane more readily then).

Plant growth stimulation by microbes

There are many more reports of the stimulation of plant growth by their (non-pathogenic) microbial associates than there are of growth inhibition (excepting for reports on the reduction of plant growth by microbial competition for nutrients (P for example) following soil amendment by usable organic materials which are low in those nutrients--and the nature of the ecological process involved is different from that under discussion here (and tends also to be temporary)). These different kinds of results appear to be valid, and this suggests that the kind of effects that microbes have on plants which they are near are dependent of the species of microbe(s) involved as well as on other factors. Kloepper, Schroth, and Miller (1980), for example, wrote a nice paper in which they reported the results of their experimentation with the effects of a fluorescent Pseudomonas sp. on potatoes. In the greenhouse they found 500% higher productivity in bacterized plants after the first 2 weeks (post-emergence), and measured a 17% increase in Pseudomonas bacterized plants in the field. They double-marked their experimental bacterial population with resistance to rifampicin and nalidixic acid, and as a result were able, at the end of the experiment to

determine the size of the populations of the strain which they had added. These turned out to be much higher than is usual in populations of bacteria added to crops in the field.

Brown (1972) isolated a number of bacteria from the rhizoplanes and rhizospheres of wheat plants and tested them for the production of plant stimulating compounds. She found that the bacteria which were competent to produce these growth stimulating materials were most common on the older roots of the wheat. The growth promoting substances produced by the bacteria she isolated and grew gave results similar to those of gibberellins and indolyl-3-acetic acid. She found that, by contrast with the activity of the bacteria found on the older roots, when 6 day roots were sampled, bacteria grown from them produced a maximum of growth inhibiting substances. Brown found that Flavobacterium, Brevibacterium, and Pseudomonas produced plant growth stimulating substances, while Pseudomonas, Achromobacter, Alcaligenes, and Brevibacterium (along with several unidentified spp.) produced inhibiting materials. Some bacteria simultaneously produced both (which could be separated by chromatographic methods), a situation which could easily cause difficulty in the interpretation of various tests, and with small change in conditions, very possibly could reverse the results. It also should be kept in mind that many experimenters who have worked with systems of this

kind use seedlings (for the good reasons that they tend to be uniform, they are small and easy to handle, seeds are relatively easy to sterilize, and it is difficult to keep plant-soil or plant-nutrient medium systems sterile or gnotobiotic for long periods).

Various workers have concentrated on the observation of one or more of the plant growth hormones which are produced by bacteria which are found on the rhizoplane or in the rhizosphere. Frequently the microorganisms are isolated and grown in a nutrient medium, after which the medium is tested for the presence of the hormone(s). Phillips and Torrey (1972), for example observed cytokinin production by Rhizobium, Barea and Brown (1974) found that Azotobacter paspali cultures contained indolyl-3-acetic acid, 2 cytokinins, and at least 3 gibberellins. A. paspali was used as an inoculum for seedlings of Paspalum notatum, Centrosema pubescens, lettuce, tomato, wheat, and Lolium perenne. Survival of the bacteria was not very good, nevertheless it apparently was enough, as the all of the plant species produced roots or shoots of significantly greater weight when inoculated than that of the controls. In most instances both root and shoot were significantly larger and heavier in the bacterized plants. The tomatoes were not weighed, but the photograph provided shows a very convincing size difference in the same direction. For those plants which were weighed 8 weeks after the beginning of the experiment, the weights of the

bacterized plants (root + shoot) were the following percent of the non-bacterized plants of the same species: L. perenne=144, wheat=167, lettuce=153, C. pubescens=171, and P. notatum=268. It may be meaningful that the plant which had the greatest increase as a result of the addition of the bacteria (and the degree of its stimulation was strikingly above the others) was Paspalum notatum, the grass from the roots of which the bacterium used was obtained. In a review paper written at about the same time (1974), Brown suggests that bacteria which produce growth promoting substances may be especially useful in the stimulation of root and leaf crops (carrots and beets, lettuce and cabbage) because photosynthate is used in these directly and immediately to increase the stored carbohydrate supply -- there is no flowering and fruiting process, with its perhaps critical timing requirements, to interfere.

Maddox and Richert (1977) worked on a method for maximizing the production of gibberelic acid by Fusarium moniliforme, and Lindsey and Baker (1967) found the weight of dwarf tomatoes to be significantly greater when grown with Trichoderma viride, Rhizopus nigricans, and Fusarium roseum than when without any of these fungi. (However, Chaetomium sp. did not have any stimulatory effect.) The differences in weight were seen in the shoots, but not in the roots. Lindsey (1967) also grew tomatoes with and without soil microorganisms and found the axenic plants to

have lower weight than the others. Hameed and Couch (1972) grew Tagetes (marigolds) with Penicillium simplicissimum and axenically, and found that those which had the fungal companions had greater size and weight and flowered earlier. They also point out that after 34 days, colonization of the roots, and degradation of them by P. simplicissimum was extensive (the increased plant weight occurred in spite of this).

Fahy (1978) added Bacillus DD32 to wheat and clover in pots in a greenhouse. He obtained an increase in grain yield of from 13 to 23% in the wheat, and of total dry weight yield of 23 to 50% in the clover. Finally for this section, Van Staden and Dimalla (1976) in a review, tell of cytokinins being detected under conditions in which they must have been released by mycorrhizal fungi, Rhizobium, Lycoperdon sp. (associated with Pinus patula), and Scleroderma sp. (associated with Carya illinoensis). The conclusion of this section is that some bacteria and some fungi can considerably increase the yield of many plants (including many crop plants) by the plant growth substances which they produce.

General nutrient uptake stimulation by microbes

There is no question but that many of the microbial species found in association with the roots of plants play important roles in "helping" the plant to obtain nutrients which otherwise would be less available. They may do this

by changing conditions of redox potential, pH, level of chelating compounds, level of enzymes which act to bring about the release of needed plant nutrients, and so on. A variety of mechanisms will be considered next within the context of discussions of some of the more important plant nutrients.

Phosphorus mobilization (except by mycorrhiza)

As is clear from a number of studies which will be discussed below, the microbiota of the rhizoplane and rhizosphere frequently are important in the making of P available to plants; however there is less evidence concerning the ability of plants to produce compounds which are particularly effective in the mobilization of P. Release of CO₂ from root respiration, will of course lower the pH in the vicinity of the roots and may result in an increase in the solution of some of the P containing compounds within the soil. It is well known that the normal microbe-root system of a number of plants produce phosphatases which are especially effective in the mobilization of P such that the plant can use it. Most work, however, has not been done in such a way that the contributions of the roots to the phosphatase production of the system can be separated from that of the microorganisms. McLachlan (1980a and b), however, in what appears to be careful experimental work, has grown rye, subterranean clover, buckwheat, and wheat axenically and

found that the roots of these species produce appreciable quantities of phosphatases. These turn out to be acid phosphatases (in contrast to the alkaline phosphatases which frequently have been reported from microbe-root systems) which have their optimal activity when the pH is in the vicinity of about 5 to 7. McLachlan further reports that these plants show considerable increase in the amount of root-produced phosphatase when they are stressed by low P availability in their nutrient medium (they were grown in liquid culture).

McLachlan used an unknown bacterial contaminant to test the effect of a microbe-root system on the production of phosphatase. He observed that there was a slight increase in the enzyme when the bacterium was present (compared to that produced by axenic roots), but the difference was not enough to reach significance at 5%. One problem with this part of the work reported by McLachlan is that one cannot generalize very much from it because only one plant was used (rye), and more importantly because only one bacterium was used and this bacterium was an unknown which was used primarily because it was convenient, and not because it had any known relationship to the mobilization of P in a mutualistic relationship with plant roots. On the other hand, he did examine the Pase productivity of the bacterium and found that P mobilizing enzymes were produced (and that they also were acid phosphatases with pH optima of about 5).

In sum, it is clear from McLachlan's work that (at least some) plant's roots produce phosphatases which presumably can be important in the increase of the availability of P to the plant.

A large number of studies have shown that the presence of a microbial community around plant roots increases the amount of P that the plants will take up, and frequently there is a concomitant increase in the growth of the plant. To examine one aspect of this problem, Greaves and Webley (1965) compared the number of microorganisms in the bulk soil and those on the rhizoplane and in the rhizosphere with respect to ability to break down an assortment of P containing organic compounds. They found much higher numbers of microorganisms capable of releasing the P from these compounds on and near the roots than in the bulk soil. The data which they report indicate that from 54% to 90% (with a mean of 71%) of the rhizoplane/rhizosphere organisms which they were able to investigate (isolate) produced phosphatase.

Rovira and Bowen (1966) and Bowen and Rovira (1966) reported that P uptake by wheat, tomato, and subterranean clover roots is greater when they have been growing in a solution which has been inoculated with soil microorganisms than when they are axenic. However, the wheat roots (7 day old) were of lower weight in the culture solution containing the microorganisms, although 5

day tomato roots and 8 day clover roots were of the same length when grown under the two conditions. It is not possible to be sure from the data presented whether or not the increased P uptake by non-sterile roots was a result of uptake by the roots themselves, or may have been partially the result of bacterial uptake (with the bacteria remaining on the root surface through the washing process).

In a study of the effects of a microbial flora on the phosphatase levels of soils, Boero and Thien (1979) found Pase to be most concentrated near to the roots of corn, and to decrease as the distance from the root increased. In plant-soil systems which had been fumigated (and had microorganism levels reduced by about 2 orders of magnitude), measured Pase levels were about 1/3 what they were in non-fumigated soils (and 3 soils of rather different characteristics were used in the experiments). Nevertheless, Boero and Thien conclude that utilization of P derived from the organic compounds which the Pases could attack was no higher in systems with roots and microorganisms than in those with roots alone. They suppose that the reason for this is that the organic compounds containing P which are in the soils already were saturated with Pases, and therefore that the addition of more Pase did not increase release rates of P. Although this conclusion coincides with those of some of the other workers, in the context of other observations, and when

one considers the fact that it would not be to the plant's selective advantage to produce Pases that did not do that plant any good (but cost it something), this conclusion does not appear to be a good one. The final statement that Boreo and Thien make in their paper is not much more appealing ("Apparently the role of plant-released phosphatase is merely to increase the reserve enzyme level in the soil"). It seems more probable that some of the time, at least, the Pases produced by the plant and by the microorganisms serve the important function of providing more available P to the plant (and the microorganisms).

Moghimi, Lewis, and Oades (1978) worked with maize, wheat, and peas, and found that the wheat was more efficient than the other two in the release of available P from synthetic hydroxyapatite (although Fe and Al phosphates were not caused to make their P available by this process). The system contained a microbial community, and it was observed that the release of the P from this calcium phosphate was associated with a drop in pH. Moghimi, Tate, and Oades (1978) used a variety of chromatographic and other techniques to examine the compounds in the soils around the roots of young wheat seedlings, and concluded that the release of P from the hydroxyapatite resulted from the production and activity of 2-ketogluconic acid. Their estimate was that about 20% of the water soluble organic product of the root-microbe system in the rhizosphere was 2-ketogluconic acid and that

this was manufactured by members of the microbial community from glucose exuded by the wheat's roots.

In work with a rather different system, Alva, Larson, and Bille (1980) observed that young rice plants in flooded soil (with help from associated microbiota?) remove P from the soil. Later, as the plants become larger, and their influence on their own environmental conditions greater, ferric phosphate precipitates around the rice roots (the plants supply oxygen via their roots, which raises the redox potential enough that FePO_4 is produced). It is, of course, the activity of the microbial community which uses the oxygen of the water-saturated soil by its respiration and reduces its redox potential sufficiently that the iron is in the ferrous state in the bulk soil, and as a result the P is not "trapped" by the iron.

Mycorrhiza and P uptake.

The greatest amount of activity in the current literature with respect to the increase in uptake of P by plants which is mediated by microorganisms associated with them is concerned with the dynamics of various fungi, called mycorrhiza, which live on and/or in the roots of the majority of species of vascular plants. In a review, Smith (1980) summarizes the current state of our understanding of these fungal-higher plant mutualisms. She starts out with the observation that there are several

distinct catagories of symbioses gathered together under the term "mycorrhizal". In this interrelationship between the two very different species, there do not appear to be what might be called disease symptoms - - rather, frequently the host (the higher plant) clearly benefits from the association as demonstrated by better growth than otherwise would be possible ("mycorrhizal plants are bigger").

By far the most frequently discussed activity of mycorrhiza is that of the increase of the availability of P to the host (although increase of N and of various cations also may occur). The papers which report on increase of host weight or growth rate, or which are concerned with which of the vascular plants frequently (normally) are hosts to mycorrhiza are numerous, and a few examples are all that can be mentioned here. O'Bannon, Evans, and Peaden (1980) examined the response of 4 strains of alfalfa (Medicago sativa) to 5 species of mycorrhiza, and found that all of the cultivar's growth was enhanced by the fungi. Ocampo (1980) was interested in the effect of crop rotations on the degree of development of (vesicular-arbuscular) mycorrhiza on the crop plants. He observed an increase in the infection rates of the hosts only when the preceeding crop was a host to the same mycorrhiza. On the other hand, the planting of non-host crops did not cause a decrease in the infection rate. The situation is not wholly

straightforward, however, as it appears that lettuce shoot dry weight may be larger when the previous crop is lavender (rather than lettuce). This suggests that one of the host plants in the experiment (lavender) was a better host than the other (lettuce) in the sense that more mycorrhiza were left in the soil after harvest (to infect the next crop).

In an important paper, Pope (1980) used an experimental design which allowed him to measure the weights of roots, stem, and leaves of sycamore (Platanus occidentalis) seedlings when they were infected or not by the mycorrhizal fungus, Glomus fasciculatus, and under 4 different levels of nutrient (he used plain water and 1x, 2x, and 4x Hoaglands solution). Pope observed that his sycamore always were stimulated (had significantly higher weight), irrespective of the concentration of the nutrient solution, when the mycorrhiza were present. Also, and of considerable importance, the maximum weight of the plants was highest when 2x Hoaglands was added to the soil. These results show (assuming Hoaglands solution to be, as it is supposed to be, a fully competent nutrient solution) that the mycorrhiza are helpful to the host even when mineral nutrition is optimal (note that, according to the plant weights, 4x Hoaglands is above optimal concentration).

Some of the recent literature concerning the effects of mycorrhiza specifically on P availability to the hosts

will be considered next. In some of the earlier work, the emphasis was on whether or not mycorrhiza would or would not help the host. Khan (1975) reported that wheat seedlings which were infected with mycorrhiza had three times the growth that non-infected seedlings had on a soil which was low in available P. On the other hand, when adequate fertilizer was used, there was no difference between the infected and non-infected plants. In a study of the distance over which mycorrhiza might be useful to plants in the obtaining and transporting of P to the roots, Rhodes and Gerdemann (1975) were able to observe the transport of radioactive P to onion roots from at least 7 cm away.

In an examination of some of the kinds of compounds from which P was removable by mycorrhizae, Barrow, Malajczuk, and Shaw (1977) observed that those into which $\text{PO}_4\text{-P}$ became incorporated at higher temperatures (70°C) held the P so strongly that the mycorrhiza could not extract it (they called this fraction the firmly bound P). Azcon, Barea, and Hayman (1976) carried out experiments with lavender and rock phosphate in which they found two different mycorrhiza to allow the host to grow better than non-mycorrhizal plants. Several bacteria were also used in their tests (and one of these when added alone, provided for increase in plant weight), and while the effects of one of the mycorrhiza were not modified by the presence of bacteria, plant weight was greater when the

other mycorrhiza and bacteria were inoculated together than when either was added alone.

Saif and Khan (1977) found that in low P soil, the addition of mycorrhiza could considerably increase the yield of barley (up to 4x), but, as many others have observed, the amount of yield increase went down as the P fertility of the soil is raised. In high P soils, not only do the mycorrhiza not make any difference to plant yield, but the population size of the fungus is reduced. In somewhat similar work with soybeans, Asimi, Gianinazzi-Pearson and Gianinazzi (1980) observed high increments of increased growth with the addition of mycorrhiza to P poor soils, and an increase in the growth of the plants (and decrease in the amount of growth stimulation by mycorrhiza) as soil P levels were increased.

Also, in soils of moderate to low P, either the addition of mycorrhiza or of available P caused an increase in the rate of nitrogen fixation by the Rhizobium in the soybean root nodules. An interesting gradient was seen in the effects of added P: when no P was added to the soil, mycorrhizal presence stimulated plant growth, nodule formation, and nitrogenase activity, at .25 g (per kg of soil) of potassium dihydrogen phosphate addition to the soil, the positive effects of mycorrhiza on plant growth was eliminated, at .5 g phosphate addition, the effects of mycorrhiza on root nodulation were suppressed,

and at 1.0 g phosphate the stimulation of nitrogenase activity by the fungi no longer was observed. Also, as the amount of P added to the soil increased, the amount of root infection by the mycorrhiza was diminished.

It appears that at least part of the reason for the increase of the P available to the plant because of its mycorrhiza is because of the high levels of phosphatase produced by the fungi (Calleja et al, 1980). However, the interaction between potential host plants, potential mycorrhizal species (strains?), and environmental conditions (including levels of variously available P in the soil) is complex, and the outcome may be easily modified by change in any of these. Mosse (1977), for example, in one of an extended series of papers on these topics, examined the interaction between different soils (which had different original P levels and different numbers and kinds of mycorrhiza in them), different levels of added rock phosphate, and the host plants Stylosanthes guyanensis and maize. In addition to results which are similar to those which are pertinent and discussed above, she found that there was an interesting interaction between the mycorrhiza native to the soils which she used and the test strain which was her inoculum. Most of the soils had relatively low P contents, and as a result the fungal species living there were not adapted to even moderately high levels of P. Many of them were competent to infect and stimulate the test host plants when the soil

did not have additional fertilization. On the other hand, the strain which she used as an inoculum was derived from agricultural soils, and therefore had a relatively high tolerance for P. It was able to do fairly well under increased fertilization levels. As a result, although the endogenous mycorrhiza did well when the soils were not fertilized, and could infect and stimulate the hosts, when P was added their populations tended to suffer and they were more easily replaced by the strain from the agricultural soil. Mosse's results (not all of which have been outlined here) make it clear that the system is complex. It is also clear that it is not yet completely understood (and we may be some considerable distance from that goal).

As a summation of the above discussion (and the literature), under a number of circumstances bacteria and fungi (especially mycorrhiza) frequently play important roles in the mobilization (and sometimes transport) of phosphorus to the roots of plants. The importance of these activities will be diminished if care is taken to always have adequate P, in forms which are available to the roots in the soil/culture medium. Even then, however, it would appear from some of the work which has been done on this problem (Pope, 1980, provides an especially nice example) that inclusion of microorganisms may significantly increase the yield of the plants.

Nitrogen cycling and plant nutrition.

Because of the gaseous nature of some of the compounds which are important in the nitrogen cycle (NH_3 , nitrogen oxides, and especially N_2), the organisms which use nitrogen compounds share a single world pool of that element. The major processes in the dynamics of the world's nitrogen cycle have to do with the processes of nitrogen fixation and denitrification, both of which are largely carried out by microbial activities.

Soderlund and Svensson (1976) provide a reasonably current review of what is known about global nitrogen cycling, and Rosswall (1976) gives finer details concerning the cycling between microorganisms, the soil, and the plants. One of the more interesting discussions in Rosswall's paper considers the change in levels of nitrogen content of cultivated and pasture systems following the beginning of each use (and each previously was the other). What happens is that there is a striking decrease in soil nitrogen with time in the cultivated soil (which originally was grassland or pasture), and it would appear from his fig. 3 to be reduced to about 1/2 of its original value in somewhat over a hundred years. On the other hand, after a previously cultivated field is put into pasture, there is an increase in soil nitrogen (which appears to take about the same amount of time to reach equilibrium, and that equilibrium is at about double the original level of nitrogen). These and other kinds of

data led Cole and Heil (1979), in their nice review, to conclude that the amount of nitrogen which will be found (at equilibrium) within a soil (as a result of the pattern of the relationship between rates of denitrification and nitrogen fixation) will be dependent of the amount of the other important limiting plant nutrients in the soil (especially of P). The result is that, given time, the nitrogen level in soils will tend to come "into balance" with the available phosphorous (as a result of appropriate shifts in the amounts of the various kinds of microbial nitrogen transformations which occur).

Denitrification.

The level at which denitrification has been observed to occur, has, in fact, so alarmed some who are knowledgeable about the matter that several papers have been written warning us about the problems which this denitrification may cause. See, for example, Payne, Rowe, and Sherr (1980) who "plea for attention" to the problem because they consider it to be so serious. The problem is that denitrification causes considerable loss of fertilizer which costs considerable money (and energy) to manufacture and to apply to the fields.

Nitrogen fixation

Because nitrogen limitation is one of the most important factors limiting yield of the world's crops, and

especially in the light of the rapidly increasing cost of man-made nitrogen fertilizer, the amount of work which has been done in recent years on biological nitrogen fixation is large and continues to grow. There will be space for only a very brief review of some of the pertinent aspects of this process here (for more information see any one of the recent reviews or collections of papers such as the volumes on "Nitrogen fixation" edited by Newton and Orme-Johnson (1980)).

Fixation by free living species

Nitrogen fixation is carried on by some blue green algae (cyanobacteria) and some bacteria. In general it requires absence of (or low levels of) oxygen to occur, as the critical enzyme, nitrogenase is oxygen sensitive. Some of the species which carry on nitrogen fixation have mutualistic relationships with plants, and some of these are to be found in specialized structures on the leaves, or especially on the roots of the host plants. These structures aid in the protection of the contained microbial populations from oxygen levels which are too high; frequently there also are biochemical mechanisms (of plant and/or microbial origin) which also aid in localized oxygen level reduction. The plants also supply nutrients to their nitrogen fixing associates (mutualists).

The phylloplane of a number of plants, especially those which grow in areas which are wet or moist

frequently or for extended periods frequently bears blue green algal and/or bacterial flora capable of fixing nitrogen. Jones (1976), for example, found a number of nitrogen fixing bacteria on leaves of fir, hemlock, larch, cypress, pine, spruce, alder, beech, oak, and sycamore in Grizedale forest of the English Lake District. Fixation was highest in the spring, with a secondary peak in late fall-early winter. Sadykof and Umarov (1980) observed that about 15% of the total nitrogen fixation which occurred in observations of wheat, fescue, and timothy was as a result of activity of phylloplane organisms (the remainder was in the rhizosphere). Tropical palm leaves (and many others) in wet forests have especially well developed leaf-dwelling microbial communities. Bentley and Carpenter (1980) experimented with the effects of drying and re-wetting of leaves of some wet forest plants and found that nitrogen fixation capacities of the leaf microcommunity developed rapidly after dry leaves were re-wet. Stimulation of the growth of Linum usitatissimum (flax) radicle length was observed by Lovett and Sager (1978) when they added leaf washings from Camelina sativa (false flax). When they analysed the causal mechanism they found that the growth stimulation resulted from a provision of available nitrogen to the flax, and that this was produced by free-living nitrogen bacteria of the false flax phylloplane community. Furthermore, the bacterium responsible for this nitrogen fixation was Enterobacter cloacae, which also has been isolated from rhizospheres of

wheat and corn, surface water, sewage, and human guts. In humans, E. cloacae usually is assumed to be a secondary pathogen. E. cloacae also has been implicated in nitrogen fixation in the guts of animals and humans. This interrelationship also illustrates again the immense interactiveness of the ecological system and (again) ties together various aspects of this paper.

The long term continuation of a relatively high fertility of many of the rice paddy soils of the far east has frequently been (partly) attributed to the input that nitrogen fixation by blue green algae make to the system. Witty et al (1979) found the nitrogen fixation of blue green algae of wheat fields to be surprisingly high. They claim that the 21% or so soil cover of blue greens which developed after the wheat is harvested contributes some 25-28 kg nitrogen/ha/yr on plots which were fertilized (48 kg fertilizer/ha), but less than that on unfertilized plots (13-19 kg nitrogen/ha). They estimate that about 30 kg/ha are added to some plots which they studied, and that only about 2-3 of this came from bacteria (and about 5 came from rain). It will be interesting to watch the development of more data on both the tropical paddy rice and terrestrial (tropical and temperate) blue green algal input through nitrogen fixation.

Free living bacteria of the rhizospheres of a number of plants may also be important for the nitrogen that they fix, although their efficiency is considerably less than

that of the bacteria which are found in root nodules (Gutschick, 1980).

There has been considerable recent interest in species and communities of free-living microorganisms which fix nitrogen in the rhizosphere of plants, especially of grasses (because the major food plants of most of the world are grasses). Some of the papers about this are by Dobereiner and Day (1975), Tow and White (1976), Rao (1978), Whitehead et al (1978), van Berkum and Bohlool (1980), and McClung and Patriquin (1980). The bacteria which are listed as showing nitrogen fixation by these papers include Azospirillum brasilense (= Spirillum lipoferum), Clostridium, Arthrobacter, Azotobacter beijerinikii, and Campylobacter. It is of interest that both the Arthrobacter and Azotobacter were stimulated to higher levels of nitrogen fixation when a Pseudomonas also was present than when they were alone (and it appears that there are probably many other kinds of interactions of this general kind which occur). In addition to the nitrogen fixation for Azospirillum brasilense (= Spirillum lipoferum) which was mentioned above, Gaskins and Hubbell (1979) found that millet (Pennisetum americanum) growth was stimulated by the production of the plant hormones kinetin, gibberelic acid, and indole acetic acid by A. brasilense. The last mentioned of these hormones (IAA) is inhibitory, but its effect was more than compensated for by the stimulatory effects of the other two. The

stimulation by the hormones appears to have more effect, at least in these systems and under most conditions, than does the production of fixed nitrogen by A. brasilense.

Trolldenier (1977) pointed that bacteria capable of nitrogen fixation make up a large proportion of the rhizosphere microbial flora of lowland (flooded) rice. He went on to report that there was a typical decrease in nitrogen fixing activity at 21% oxygen, but that as the O₂ level fell there was an increase in fixation until oxygen became rather low. However, when the oxygen was completely gone, fixation rates were somewhat reduced in comparison to their levels at 3% oxygen. Furthermore, as is the situation with symbiotic nitrogen fixation, there appeared to be a link between the production of photosynthate by the plant and the fixation rate. After there had been a favorable period for the plant to carry on photosynthesis, and time for carbohydrate to be translocated to the roots, there was an increase in fixation rate, presumably in response to the increased bacterial substrate supply via the exudation of organic materials by the plant roots. Livingston and Patriquin (1980) also report a change in the amount of fixation by Azospirillum associated with the roots of the grass, Digitaria decumbens, as the plant shifted from vegetative to reproductive growth (it increased by about a factor of 3).

Symbiotic nitrogen fixation (in nodules)

There are some nodules which form on leaves (and contain bacteria), but they as yet have not been shown to fix nitrogen. A number of groups of plants develop root nodules with various kinds of microorganisms in them and with the ability to fix nitrogen. As Gutschick (1980) reported, and as one would have predicted from theory, efficiency of fixation is generally higher in microorganisms in nodules than in the free living microbiota. Considering the amount of fixed nitrogen produced and the amount of glucose required, Gutschick estimates that in-nodule fixation is around 18% efficient (similar efficiencies for free living microorganisms was estimated to average about 3%). Phillips (1980) agrees fairly closely with Gutschick's estimate. He calculates that whole plant efficiency (for symbiotic fixation in legumes) is such that about 6.5 g of carbon (as carbohydrate) is required to fix a gram of nitrogen.

Alder (Alnus), Camptonia, and other species have root nodules harboring nitrogen fixing actinomycetes (Roelofsen and Akkermans, 1979, and Tjepkema, Ormerod, and Torrey, 1980). By far the best known, of course, is the association of the nitrogen fixing bacteria Rhizobium with (and in root nodules of) a wide variety of the legumes. Studies of this system are numerous, and only a few will be mentioned here to give an overview and entree to the literature. Vidor and Miller (1980) have been concerned

with the survivability of Rhizobium japonicum in 2 different soils. In both of these the numbers of the bacteria increased after inoculation when the soil had previously been sterilized (by autoclaving - - which also may have had an additional effect of providing additional bacterial nutrient by the cooking which occurred). In both of the soils, when they had not been sterilized, the number in the Rhizobium population decreased after inoculation. It appears that competition by the saprophytes of the soil (which are probably more efficient at obtaining nutrient when its level is low), and possibly attack by bacteriophage were important in causing this fall in the size of the Rhizobium population.

In a somewhat related study, van Egeraat (1978) observed that, while pea roots produce 2-alanyl-isoxazolin-5-one which appears to inhibit the growth of the pea rhizobium (Rhizobium leguminosarum), the relatively large amounts of homoserine which is released during the penetration of the main root by the lateral roots more than overcomes that inhibition and in fact specifically stimulates the rhizobium. In a review of the interactions between Rhizobium and its hosts, Schmidt (1979) points out that data on the survival of the bacterium in the rhizosphere are "virtually nonexistent". Schmidt goes on to consider the nature of the interaction which permits the "proper" species (strain) of Rhizobium to recognize its "proper" host. It is clear that there

are very specific interactions involved (recall that some of these were outlined in the section, above, on pathogenesis). Stacey, Paa, and Brill (1980) have shown that there are lectins on the pole of the cells of R. japonicum which bind the bacterium, with a very high specificity to the roots of their host, soybean. After the Rhizobium "selects" its proper host it invades the roots via root hairs, stimulates formation of nodules to occur, and within the nodule transforms to a different morphology. Then it is ready to carry on nitrogen fixation. There is a nice story about the mechanisms of nitrogen fixation, including the biochemical one of the production of a leg-haemoglobin (by the plant's tissues!) which protects the rhizobium's nitrogenase from destruction by oxygen, but we will go now to consideration of some of the ecological factors which affect the rates of fixation within legume nodules.

The rate at which carbohydrates are made available to the Rhizobium of the nodules has great effect on the rate at which nitrogen fixation is carried on (Minchin and Pate, 1973 & 1974). In experimental work with peas, they observed an increase in fixation rate (as measured by acetylene reduction), respiration rate, and sugar level of nodule tissues as the light period progressed (and increasing amounts of photosynthate were being delivered to the nodules). Export of fixed nitrogen from the nodules was enough higher during the day than in the

night, however, so that even though fixation increased during the day, the size of the fixed nitrogen pool of the nodules decreased. There was a reversal of all of these trends during the night, and clipping of the shoot also caused the rate of photosynthate production, and following that the rate of nitrogen fixation, to fall. Minchin and Pate also made up nice carbon and nitrogen budgets for their plants, and were able to also provide estimates of the water cost of nitrogen fixation. Their estimates of the relative costs of nitrogen fixation and on nitrate reduction (to ammonia) were similar to those of Gutschick which were discussed above. (Minchin and Pate give the following data: 5.9 mg C respired per mg nitrogen fixed, 6.2 mg C respired (in non-nodulated roots) per mg of nitrate reduced to ammonia, and the nodules require 4.1 mg C (=10.3 mg carbohydrate) for growth, their respiration, and export for each mg of nitrogen fixed.) Sheehy et al (1980) kept soybean and alfalfa in the dark for 40 hr., and then measured their nitrogen fixation rates under two levels of atmospheric carbon dioxide. It took several (soybean) to many (alfalfa) hours for the fixation rates to approach their maximal values, and the steady state fixation rates were higher in the high than in the low carbon dioxide conditions. Houwaard (1980) also measured fixation (in detached nodules from pea roots) as a function of the nature of the chemical substrate provided. He found that a fairly wide variety of compounds supported some fixation, but that succinate, fumarate, and malate

were most effective. Also, the addition of ammonium chloride, which was shown not to influence the nitrogen fixing activity of isolated Rhizobium bacteroids, was effective in the inhibition of fixation within the detached nodules. There may be some problem with the technique involving the use of detached nodules, as Houwaard's analysis indicates a lower than usual fixation efficiency (16 g of carbohydrate per g fixed nitrogen). The results do suggest, however, that the reduction of fixation which occurs upon nitrogen fertilization may be mediated through the tissues of the nodules rather than being a direct response of the Rhizobium cells.

In this respect, Bethlenalvay et al (1978 a & b) observed that with low available nitrogen, fixation by the Rhizobium of peas was greater than when there was no nitrogen (NH_4^+) in the root medium, and with increase of availability of nitrogen to the roots beyond 2 mM NH_4^+ , fixation then decreased. When the ammonium was greater than 8 mM, the possession of a nitrogen fixing system was disadvantageous (plants without Rhizobium had higher nitrogen content and dry plant weight). Bethlenalvay et al also examined the rates at which different strains of Rhizobium leguminosarum carried on nitrogen fixation, and found considerable variability (the highest rates were 6 times the lowest).

Not only do bacteriophage sometimes influence the amount of nitrogen fixation which may occur in a legume-Rhizobium association by considerably reducing the infection rate, but there are other interrelationships between nitrogen fixation and non-symbiotic bacteria which affect fixation rates. One of these is exemplified by the work of Vlands, Barnes, and Frosheiser (1980) in which alfalfa was selected (from a single original gene pool) for high and low nitrogen fixation rates (in conjunction with its appropriate Rhizobium strain). After a couple of generations of selection there were distinct differences between the differently selected populations with respect to nitrogen fixation rates (and in the directions expected), but when the selected strains were tested for resistance to the bacterial wilt caused by Corynebacterium insidiosum, it was found that there was a strong negative correlation between the ability to fix nitrogen and the ability to resist the attack of this bacterium. On the other hand, the level of nitrogen fixation rate did not affect the resistance to two other pathogens of alfalfa, Phytophthora root rot, and Fusarium wilt.

In the context of the development of a better way to grow peas and their Rhizobium such that very good control can be exercised over the environmental conditions at the root surface, Evans, Lewin, and Vella (1980) developed an aeroponic (water spray) system which could be used. With this they obtained data which show that the rates of plant

growth and of nitrogen fixation were greater at a pH of 6.6 than at lower pHs. There were few nodules and little nitrogen fixation below a pH of 4.8. (Their curves, however, are somewhat strange, and need to be verified and made more complete.)

The problem of production of hydrogen might become of importance in closed systems in which biological nitrogen fixation is going on. Nitrogenase reduces water to produce hydrogen (as well as breaking the N-N bond during fixation). This is true in blue green algal, alder-actinomycete, and legume-Rhizobium systems. Conrad and Seiler (1979) have examined the production of hydrogen by fields of Trifolium dubium, and found that about 30% of the Nase electron flow was used to reduce protons to H_2 . It is therefore possible that much of the H_2 in the earth's atmosphere is a result of nitrogen fixation "side reaction". In any event, some kind of hydrogen sink will be required in a closed system carrying on much nitrogen fixation (this may not be a difficult problem, as there are a number of bacteria which use hydrogen).

Mobilization of other mineral nutrients

A number of mineral nutrients of plants (in addition to those discussed above) frequently are present within an area but unavailable to the plants because they are very insoluble. Arrieta and Grez (1971) examined the interaction between 81 different microorganisms and

granodiorite containing iron. Six different iron-containing minerals were then placed in cultures of the 10 most active of the fungal species from the preliminary test, and Arrieta and Grez observed that iron was solubilized from each of the minerals by each of these fungi. In another investigation of iron nutrition, Marschner and Barber (1975), however, found that the presence or absence of microorganisms appeared to make no difference in iron availability to sunflower. These plants (with or without microorganisms) were able to remove iron from FeEDTA and from ferric compounds by bringing about a lowering of the pH and producing reducing organic substances and riboflavin (when under iron scarcity stress).

In a study of the reasons that some strains of the bacterium Pseudomonas fluorescens-putida were competent to increase the yield of some crops (up to 144%), Kloepper et al (1980), in a very nice study, unraveled a somewhat complicated system in which iron was important. What happens on the inoculation of potato, sugar beet, and radishes with the pseudomonad is that it rapidly colonizes the roots and prevents the growth of Erwinia carotovora (which causes potato root rot and seedpiece decay). The pseudomonad is effective only when the level of iron in the medium is not too high, as the root rot inhibition mechanism functions through the production of a siderophore which takes up the iron and holds it so firmly

that it denies it to E. carotovora. The inhibition of the erwinia does not occur when large enough quantities of iron are added (with the result that there is still some available iron left after the siderophore of the pseudomonad is iron-saturated). In a test of this hypothesis as it was derived from the data just summarized, the interaction of this strain of the pseudomonad with two different strains of Escherichia coli was observed. One of these strains of E. coli produces its own powerful siderophore, enterobactin, and this strain was not affected by the presence of P. fluorescens-putida. The other E. coli does not produce enterobactin, and it was inhibited by the pseudomonad unless enough iron was added to more than saturate the pseudomonad's siderophore; furthermore, a mutant of the P. fluorescens-putida which did not produce the siderophore was not inhibitory to E. carotovora.

Manganese also can be taken from MnEDTA by soil microorganism-plant systems more effectively than be plants alone, and uptake of S, P, Mo, Zn, Ca, and K also can be mediated under some conditions by various of this microbiota (see Barber, 1978, for a review). On the other hand, the soil microorganisms may compete with the plants for the nutrients. In addition to the examples discussed above with respect to N and P, Lee and Loutit (1977) have demonstrated that the polysaccharides which are produced by various of the rhizosphere microorganisms, Pseudomonas

aeruginosa for example, can bind Mo and reduce its availability to radish plants.

Decomposition

In addition to their activities in the general decomposition of organic materials, various of the microorganisms of the soil are particularly adapted for the decomposition of especially recalcitrant and/or toxic plant products. The overall topic is considered by the set of papers in the British Ecological Society Symposium edited by Anderson and Macfadyn (1976).

Also, Grant (1976) discusses the unusual ability of Penicillium adametzi to degrade tannins (no doubt other species also can do this). Tannins and related phenolic polymers are fairly common in nature; apparantly they have been elaborated as a plant defense against pests and pathogens. Sometimes they are produced in fairly great concentration, for example, tannins account for 50-60% of the dry weight of Pinus radiata bark, and as a result most microorganisms cannot degrade it. This is because the microbial enzymes (appear to) bind to the tannins rather than to function in their usual molecule splitting fashion. The details of how enzymes from P. adametzi degrade the tannins is not understood, but in general, they must be able to somehow avoid the inactivation mechanisms by which most enzymes are affected by tannins.

Lignin is less of a difficulty to microbial decomposition than are the tannins, but it is nevertheless quite inert, and only a limited number of soil microorganisms can attack it. Most of those which have this capability belong to the group of the white rot fungi, and Kirk et al (1978) have examined the effect of various levels of various environmental factors on the rate at which one of these white rot fungi (Phanerochaete chrysosporium) attacks (synthetic) lignin. It appears that the energy that the fungus can get from the lignin alone is not enough to support it, and therefore that other (more easily used) substrate also is required. A number of materials will serve, including glucose, glycerol, cellulose, and Na succinate. Oxygen and thiamine also are necessary. A pH of between about 3.7 and 5.3 is required for best lignin dissolution rates, although some lignin can be broken down by this species beyond this range (from about 3.0 and to about 6.0). The kind of cometabolism illustrated by this example also is necessary for the attack by microorganisms on a number of toxic organic compounds (Alexander, 1980).

Other microbial activities of probable importance.

Ethylene

For a number of years it has been known that there are a number of sources of ethylene in nature (microbial

activity of the soils, plants, burning, etc), and that ethylene may exert powerful influences on vascular plants (see Abeles, 1973, for an extensive review). A few samples from the literature can be included here. Production of ethylene by soils, for example, was shown to occur by Lill and McWha (1976), when they removed 10 cm cores of litter and soil from a mature Pinus radiata forest, sealed each of them in a chamber and flushed the chamber gently with ethylene-free air. Not only did these small cores from the forest floor produce ethylene, but the amount of ethylene evolved from them was enough to have inhibitory effects on the growth of white clover (Trifolium repens) seedlings, and have stimulatory effects on young rice (Oryza sativa). Lill and McWha were able to remove the ethylene from the atmosphere of their systems either by a cold trap or by bubbling the air through a solution of potassium permanganate.

Ethylene production was observed by Hill and Lyda (1976) in pure cultures of the fungus Phymatotrichum omnivorum, and Goodlass and Smith (1978 a & b) experimented with the effects of various soil treatments on the amount of ethylene that was produced. They found that an increase in pH from 5 to 7 resulted in a considerable reduction in the amount of ethylene evolved, and that some organic amendments to soils (but not others) resulted in an increase in the amount of ethylene produced. Also, they observed a rather striking negative

correlation between the relative amounts of nitrous oxide and ethylene produced when soil nitrate levels were different. When soil nitrate was low, there was little nitrous oxide, but considerable ethylene produced under anaerobic conditions. On the other hand, when the nitrate level was high, there was relatively little ethylene and considerable nitrous oxide (the relatively ready availability of oxygen from nitrate may have kept the redox potential from getting low enough to permit much ethylene production).

In another kind of experiment which is of considerable interest, Smith, Milham, and Morrison (1978) found that the simple addition of ferrous iron, or the production of anaerobic conditions which led to the release of ferrous iron to/in a soil led to the non-biological production of ethylene. They pointed out that the production of ethylene is inhibited by the presence of nitrate because the redox potential would be kept too high for ferrous to be produced from ferric iron. They claim that the ethylene is not produced by the microorganisms, and that the role of these microorganisms in its production is simply that of reducing the redox potential far enough that ferrous iron will be produced. At present it would appear that both direct and indirect (ferrous iron caused) production may occur. The topic certainly needs more research.

In any event, it seems that ethylene does not have a gross effect of the respiration of microbial communities (Smith, 1978), although it can have considerable effect on plants, and even may be transported from the soil, through the stem, in quantities high enough to bring about epinasty and other ethylene caused responses in tomatoes (Jackson and Campbell, 1975).

Vascular plants also produce ethylene during many of their normal processes (fruit ripening, for example, see Abeles, 1973), and when wounded (Boller and Kende, 1980). Plant flowering and other activities may be affected by ethylene -- for example, Ketring and Schubert (1980) report that it is possible to control the flowering time of peanuts (Arachis hypogaea) by appropriate use of ethrel (which decomposes to release ethylene), but that at least under the conditions they used, the yield was reduced. Long before the mechanism was understood, managers of pineapple plantations would burn grassy/shrubby areas upwind of pineapple fields to induce simultaneous flowering of the plants. As is now known (Abeles, 1973), the mechanism involved is the production of ethylene during the burning process, and its drifting across the fields, during which it stimulates the initiation of (simultaneous) flowering of the pineapple plants.

Additionally, especially if attempts are to be made to grow crops under less than 1 G, one should pay attention to the work of Wheeler and Salisbury (1980)

which showed that inhibitors of ethylene syntheses by plants also inhibit the upwards bending of tomato (Lycopersicon esculentum), castor bean (Ricinus communis), and cocklebur (Xanthium strumarium). How general this kind of response is is unknown, but these plants represent considerable systematic span, so that one would guess that it may be widespread.

Soils which contain microbial communities, frequently are sinks for ethylene when they are not anaerobic. Cornforth (1975), for example points out that at least some soils have rates of uptake which are on the order of about 50 times the rate at which they can produce ethylene. That this activity of the soil is the result of its microbial processes is supported by Abeles et al (1971) in their report that sterile soils do not remove ethylene (and removal rates of sulfur dioxide or nitrogen dioxide also are slowed) after they have been sterilized, although they will do so before that treatment. In addition, Hill and Lyda (1976) grew the fungus, Phymatotrichum omnivorum in axenic culture and observed that ethylene was produced.

Before the discussion of ethylene is closed, it should be mentioned that in closed systems it may be necessary to be careful that unexpected and peculiar sources of ethylene do not interfere. For example, Wills (1970) has reported that fluorescent lighting fixtures may produce ethylene, and it has been observed also to be

produced by the warming of the shellac which is used as winding insulation on a number of electric motors.

Volatile nitrogen compounds

Some of the work on gaseous nitrogen compounds was referred to above as being discussed by Delwiche and Bryan (1976), Soderlund and Svensson (1976), Trollidenier (1979), and Payne, Rowe, and Scherr (1980) in the context of the problems of denitrification. In addition there are movements of ammonia which should be briefly considered. Denmed, Freney, and Simpson (1976) compared the loss of ammonia to the atmosphere of grazed and ungrazed pasture. The latter lost very little, because the ammonia lost from the soil surface was taken up by the canopy, but the grazed pasture, which had a much reduced canopy, lost appreciable amounts to the atmosphere (estimated to be about 13 g/ha/hr.). Hooker et al (1980) examined winter wheat in pots (and in the field) and reported from the pot experiments that the loss of ammonia was greater than that of NO or NO₂, and that NH₃ loss very nearly tripled a short time after the wheat flowered "as the plant tissue began to senesce".

Stefanson (1970, 1972a, b, and c, and 1973) reported the increase of nitrogen oxides derived from the soil in some closed chamber studies of plants. In a study of the dynamics of the transformations in the soil of NO to NO₂, Galbally and Roy (1978) found that the half life of NO is

very different at different concentrations. At NO concentrations of 100 ppm, the oxidation of NO to NO₂ by atmospheric oxygen was half complete in about an hour, but when the NO concentration was only 0.01 ppm, this half life period was on the order of a thousand hours. They go on to describe how NO built up in their experimental chamber until it was about 16 ppb in the atmosphere, and then it no longer continued to increase in concentration, presumably because at that level of concentration there were NO destroying processes which balanced the processes of NO production. Galbally and Roy pointed out that the total loss from the soil of nitrogen as NO is considerable: from estimates of 0.16 and 0.35×10^{-11} kg m⁻² s⁻¹ loss of NO from ungrazed and grazed pastures, respectively, they derived a figure for the world for a nitrogen loss of about 10^{10} kg/yr (comparable estimates for world-wide nitrogen fixation are 2 to 3×10^{10} kg/yr.).

In other examination of the factors which determine the rates of nitrogen transformations in the soil, Blackmer and Bremner (1978 & 1979) found that low concentrations of NO₃ inhibit the transformation of N₂O to N. Also, the process does not occur at high NO₃ concentrations, as then the microorganisms will use the NO₃ as their oxygen source and will leave the N₂O alone. For more details about the interactions involving the nitrogen cycle of the microorganisms, the plants, and the

soil, see Rosswall's (1976) review.

Carbon monoxide

Green plants, when they are carrying out their normal photosynthetic and other activities during the lighted part of the day, produce but do not take up CO (Fischer and Luttge, 1978). Because the rate of CO evolution changes as does the rate of photorespiration (increases with light level, temperature, and oxygen concentration, and decreases with higher CO₂ concentration), it appears that CO production may result from some part of that process. Carbon monoxide also is produced by many other organisms (microbes, fungi, animals including man, and so on). On the other hand, CO is taken up by soils (aerobic or anaerobic), although the rate of that uptake (and presumably destruction) is strongly inhibited by a number of antibiotics (Conrad and Seiler, 1980). Also, the production of CO by the soil is stimulated by antibiotics, autoclaving, UV, and so on. These patterns suggest that in the main, the CO uptake of the soil is the result of biological processes, while production of CO in the soil is abiotic.

Volatile sulfur compounds

Under some conditions considerable amounts of hydrogen sulfide can be produced by anaerobic decay processes (and released into the atmosphere). However, it

now appears as if there also are relatively large quantities of some of the methylated sulfides, especially dimethyl sulfide, which result from biological activities and which get into the air (Granat, Rodhe, and Hallberg, 1976; Bremner and Steale, 1978).

In experimental work with aerobic and anaerobic soils which did or did not receive ammendations of S, Banwart and Bremner (1976) found that some soils did not produce volatile S compounds, and that those which did produced mostly dimethyl sulfide (with a little carbonyl sulfide and carbon disulfide). Bremner and Banwort (1976) also report on sorption of sulfur gasses by the soil. Anaerobic ("waterlogged") soils produced considerably more of these volatiles than did aerobic soils.

Anaerobic conditions

Unless a soil is rather dry or low in organic matter, it probably usually includes at least some microsites in which the redox potential is low (and oxygen absent). It may be that the production of such sites, which shrink and grow with drying and wetting of the soil, is important in aiding the mobilization of some of the minerals which plants require. In rice growing in flooded soils, as Trolldenier (1977) reports, there is a reversal of the above pattern. Here there is a shallow zone next to the rice roots which has a higher redox potential than the surrounding soil (and which in healthy rice plants is

brown rather than the typical black of the surrounding reducing soils). This is because, as pointed out above, healthy rice transports appreciable (and important) quantities of oxygen to its roots.

In a discussion of the (damaging) effects of anaerobic soils on (non-rice) crop plants growing in them, Drew and Lynch (1980) give the following list of the kinds of problems that these conditions cause plants: 1. accumulation of toxins (root and/or microbial), 2. dessication of the plant because the lowered oxygen level lowers root permeability, 3. production of hormone imbalance from leaf water stress and/or interference with root supply, 4. nutrient deficiency, and 5. attack on the roots by the microbiota. In spite of these problems, it seems likely that some of the mineralization on which the plants depend (including the availability of elements for which redox potential makes a difference with respect to availability to the plants) well may depend on the fairly frequent presence of microsites which have low redox potential. Most soils which have enough water and enough organic matter will contain such sites.

In their paper which is discussed above with respect to the production of ethylene by the action of ferrous iron on organic matter of the soil, Smith, Milham, and Morrison (1978) also describe a somewhat hypothetical but possible kind of biological oscillator: a microsite rich in organic matter becomes moistened and the water permits

the bacteria to respire at a high rate. The redox potential of the center of the site drops as a result of microbial oxygen consumption and becomes low enough that ferrous iron is liberated. This ferrous iron causes ethylene to be produced, and the ethylene diffuses out to the surrounding zone of microbial metabolic activity, and inhibits that activity (but recall that Smith, 1978, concluded that ethylene of up to 50 ppm has no effect on microbial activities). When the oxygen uptake in this surrounding zone of the microsite drops because of the inhibited respiratory rate, oxygen then can diffuse towards the center of the site where it causes an increase in redox potential and the reversion of the iron to the ferric state. When ferrous iron no longer is present, the production of the ethylene ceases, then the inhibition of the nearby microbial respiration is lifted, the microbial population uses oxygen rapidly again, and again the center of the microsite experiences a drop of redox potential, ferrous ions are produced, and so on...

This oscillatory model is still somewhat hypothetical, but it provides an example of the effects of one of the kinds of feedback process which is common in biological systems, and which must be taken into account when working with them.

Intermicrobial interactions which affect plants

Jones and Hood (1980) report an interesting interaction, which appears to be mutualistic, between an ammonium oxidizing bacterium, Nitrosomonas sp and either of two different heterotrophic bacteria, Nocardia atlantica or Pseudomonas sp.. More activity (in the production of NO_2 from NH_4^+) is seen in populations of Nitrosomas in the presence of Nocardia or Pseudomonas than when it is alone, and at the same time, the population of the heterotroph is larger than it, would be if it were alone. The magnitude of the change in population number of Nocardia with the addition of Nitrosomonas is especially dramatic - - it is a full order of magnitude.

Several nodule-forming microorganisms have been observed to have what may be mutualistic relationships with other microorganisms, or what may be a sharing with another microorganism of their mutualistic relationships with their green plant. The yields of Vigna radiata (moong), Glycine max (soybean), and Pisum sativum (pea) were increased when the inoculum of Rhizobium provided for them also included a species of Azotobacter (Jauhari, Bhatnagar and Iswaran, 1979). Also, Bowen and Theodorou (1979) report that some of the soil bacteria have inhibitory effects on the colonization of Pinus radiata roots by the ectomycorrhizal fungus, Rhizopogon luteolus. In addition, Rose (1980) has observed that 25 species of green plants from 7 families (Betulaceae, Casuarinaceae, Myricaceae, Rhamnaceae, Rosaceae, Elaeagnaceae, and

Datisceae) which have actinomycete, nitrogen fixing root nodules, also have mycorrhizal associations.

In Alnus rubra (red alder), Knowlton, Berry, and Torrey (1980) observed that invasion of the root nodule actinomycete (Frankia) very seldom occurred when only Frankia was present at the alder root surfaces. Successful nodulation did, however, occur when any one of several bacteria were present (either of 2 spp. of Pseudomonas, a Chromobacterium (?) sp., or an unidentified sp.). All of the bacteria which were successful "helpers" of the invasion of Alnus by Frankia caused a deformation of the alder's root hairs (and there were some other bacterial species which caused root hair deformation but which were not effective "helpers"). The accompaniment of root hair deformation with successful invasion of nodulating bacteria of their mutualist also occurs in the Rhizobium-legume system, but there the nodulating microorganism is competent to carry out the deformation and invasion without aid from another species.

Several reports in the literature discuss the effect of bacteriophage on the ability of various bacterial populations to maintain themselves. For example, Evans, Barnett, and Vincent (1979a & b) found that the nodulation rate of clover by Rhizobium was reduced by the presence of a Rhizobium bacteriophage in the soil; as one would expect, the number of Rhizobium which could be recovered from the rhizoplane of the clover was lower in the

presence than in the absence of the phage. A shift in the population structure also followed the introduction of the phage in that phage-sensitive strains of Rhizobium were replaced by strains which the phage could not affect as much. In the absence of the phage these resistant strains apparently were inferior competitors to the phage-sensitive strain of Rhizobium. It may be useful to mention at this point that according to Zurkowski (1980) adsorption of Rhizobium trifolii to the root hairs of its mutualist, Trifolium pratense (clover) is not possible unless the Rhizobium is carrying plasmid pWZ2. (And adsorption to the root hair is a necessary step in the process of the invasion of the plant's tissues by the bacterium.)

The human carried microbiota:

Possible effects on (usually harm to)
plants of human carried microbes.

Reports of microbiota carried by humans which may be able to invade and to harm plants are relatively few. There are also some instances of so called plant microorganisms which have been sometimes found in humans, occasionally with serious results. In addition to the reasons of sharp forces directing both human and plant pathologists to examine little more than those organisms which appear to be implicated in doing considerable damage to their hosts, there has been all too much of a

willingness to use the easy way out and tend to assume that systematics of the various microbial groups is greatly related to patterns of pathogenesis. Starr (1979), in an editorial of the Annals of Internal Medicine used the following title, which also provides summary of his complaint: "Plant-associated bacteria as human pathogens: disciplinal insularity, ambilateral harmfulness, epistemological primacy".

Starr points out that there are some 200 species of bacteria and fungi which (are known to) show some signs of causing ambilateral harmfulness -- they attack and harm both plant(s) and animal(s). Examples which he gives include: Pseudomonas aeruginosa which causes diseases in man and plants (in onions at least); Serratia spp. are common opportunistic pathogens of man, and some are harmful (if not fully pathogenic) in plants; the Erwinia herbicola group (its name when plant-associated) is called Enterobacter agglomerans by some clinicians and microbiologists -- it has members which are "harmless" to pathogenic, and which also are common nosocomial pathogens; Spiroplasma includes species which are serious plant pathogens and (the same species?) pathogens of invertebrates and vertebrates; Erwinia ananas perhaps attacks pineapples and can cause serious disease in man; and so on. Starr goes on to say "Infections in man caused by plant-associated bacteria (Erwinia, Serratia, Pseudomonas) are commonplace today." He then worries about

the changes which we cause on our normal human microbial communities by the drugs (especially antibiotics) that we take, and expresses the same fundamental kind of concern for humans that many of the preceeding sections of this report show would be appropriate for plants which were critical to us and which were deprived of their normal microbial communities. He also points out, as will be detailed more in this report below, that evolution of the various of our microbial inhabitants can be very rapid and can have very serious consequences.

Other reports which relate plant and human (carried) microorganisms include that of Cooper-Smith and von Graeveniz (1978) in which it is stated that the Erwinia herbicola (=Enterobacter agglomerans) group, which originally were thought to be only plant pathogens, "are now known to be significant human pathogens". They cause septicemia -- of 15 patients studied over 5 1/2 years with infections suspected to be caused by it, Erwinia herbicola was shown in 6 instances to be significantly correlated with the septicemia, while in the other cases, the attribution of infection causality to E. herbicola was doubtful.

Schneierson and Bottone (1973) pointed out that Erwinia is ubiquitous, and Lakso and Starr (1970) examined the degree to which Erwinia spp. and other enterobacteria are injurious to plants and animals. They examined 45 Erwinia-like isolates from animals and used 8 different

tests to assay the injuriousness of each to plants. Their conclusions were that 16 of these were not injurious, 13 only slightly so, and the remaining 16 produced as much injury (had as high composite scores) as Erwinia strains which are generally considered to be pathogenic. Of the 21 non-Erwinia-like, "non-pathogenic" enterobacteria strains which also were tested (15 spp. in 9 genera), 5 strains (4 genera, 4 spp.) had injuriousness composite scores which were higher than scores for many of the Erwinia strains which are recognized to be pathogenic. They summarized their conclusions: "some plant and animal enterobacteria, not ordinarily thought to be phytopathogenic, are indeed injurious to plants in similar ways and to the same extent as are phytopathogenic bacteria."

Sharma and Mukerji (1976) point out that Candida albicans a yeast which can be a serious human pathogen, has a "consistant occurrence...on Sesamum (orientale) and Gossypium (hirsutum)". This they point out is of considerable importance, especially as, at least on Sesamum (Sesame or Bene), it is a "well established member of the phylloplane" (microflora). This may be especially pertinent in the context of Taylor's (1974) review of "space microbiology" in which he discusses the considerable increase in the C. albicans populations of personnel of several space flights (and this development appears possibly to be the result of a reduction of part

of the normal human microbial flora which usually serves to protect the humans, through competition, from the development of large C. albicans populations).

Debette and Blondeau (1980) report that Pseudomonas maltophilia has been identified in the rhizospheres of a number of cultivated plants (cabbage, rape, mustard, corn, and beet). This has considerable significance because it also is found in water, milk, and frozen food, but most importantly, most strains have been isolated from clinical specimens (Bergey's Manual, 8th ed., Buchanan and Gibbons, eds. 1974). In a more complicated but somewhat similar way, as was discussed above, Enterobacter cloacae which usually is considered to be a secondary pathogen of humans, is found widely in nature, and frequently closely associated with plants (Lovett and Sager, 1978). This example is especially interesting, as the reader will remember, because E. cloacae fixes nitrogen in our guts and on the surfaces of leaves. Fixation on the phylloplane may, indeed, be in enough quantity to have stimulatory effects on the plants (and certainly could play a role in the operation of the nitrogen cycle of an enclosed ecosystem such as will be needed for extraterrestrial stations).

Microbiota for special functions.

Because microorganisms are small, reproduce themselves, and many of them are competent in efficiently

carrying out special biochemical processes, it may turn out to be desirable to use some of them to carry out necessary or desirable processes within human-supporting closed systems. For example, (relatively) high temperature biological reactors may be the most cost effective systems to carry out some (most?) of the waste processing-nutrient cycling which will be necessary within the system. If this should turn out to be true, then it will be necessary to examine the microbial communities which are chosen for this purpose for their possible effects on humans and on the agricultural species which are used.

There also is the possibility that it will turn out to be desirable, considering the interactive processes which are to produce the overall system function, to have some (of the) part(s) of the waste processing-nutrient cycling activity going on within a plant root medium. Other species than those used in, for example, the high temperature reactor mentioned above, would then be necessary for the operation of this part of the process, and they also must be examined for their possible affects on other parts of the enclosed system (and vice versa). How effective microbial communities derived from the normal human-carried assemblage might be in this context should be tested.

Additional species of microorganisms which may be desirable, and which will have to be considered with

respect to their possible interactions with the rest of the system include those which might function in production of desirable chemical or food materials (single cell food, alcohol, and so on), and/or which may act on raw food items to produce more useful products (the making of cheese and yogurt (if dairy animals (goats?) are to be used). Some microorganisms may be required to provide food substances (vitamin B-12, for example) not made available by the green plants which will be used. Other species may serve most effectively to provide sinks for materials which otherwise might cause problems (destruablection of methane, ethylene, oxides of nitrogen, and so on), and some may be required for complete (and most cost efficient cycling of some of the elements (nitrogen fixers, denitrifiers, and so on). Other microorganisms may provide the best mechanisms for carrying out still other important functions.

It is possible that it will be desirable to take one or more kinds of animals which can serve as food and which may be effective adjuncts to the waste disposal system in the sense that they use and modify plant materials to the point that what is left may be more readily attacked by decomposers than otherwise. Animal species chosen will, of course be herbivores which can use plant products, stems and some leaves for example, which humans cannot. Should animals be taken, it will be relatively simple to obtain adequate germfree populations, but some attention

will have to be paid to the possibility that their presence might have effects on the final microbial community which would be maintained in the system. Before the decision is made to take or not to take animals, nutritional, gustatory and satiety values, in addition to the value of their products other than food, should be carefully considered.

Microbial evolution and its implications.

A problem which sometimes leads to acute difficulties for some human beings on earth is that the capacity for evolutionary adaptation of microorganisms is great. One practical result of this is that some microbes evolve resistance to an anti-biotic rapidly. After that, the microbial species may be much more dangerous than before, and possibly may be death-dealing. Furthermore, after one species develops such an immunity, then this initial evolutionary event may be followed by the operation of mechanisms which serve to pass the resistance component(s) readily back and forth among different species of the microbial community.

The literature on these processes is very large and this is not the place to pursue it in great detail; however, evolutionary rates which are typical of bacteria vary from about 10^{-6} to 10^{-9} per cell per generation, and if one remembers that the normal number of bacteria carried by one human being is on the order of 10^{14} , it is

clear that the microbial community of any closed system containing humans will experience many mutations per (bacterial) generation, providing for a constant and substantial source of raw material on which evolutionary forces will act. In addition to mutation rates within the microbial populations, there are also other pertinent factors which will need to be taken into account. These are that the rate at which new combinations of genes within bacteria can be produced by the activities of extra-chromosomal genetic elements are much higher than can be produced by simple mutations occurring sequentially within a line of bacterial inheritance. Davey and Reanney (1980) provide a fascinating and up to date review of the processes involved. They point out that there are large numbers of genes which are known to be carried from bacterium to bacterium by plasmids and phage, and that this, for example, has been observed to permit the production of populations of bacteria which have resistance genes to four different antibiotics. If one takes the range of mutation rates which is suggested above (10^{-6} to 10^{-9}) as appropriate for single gene mutations, it then follows that the probability simultaneous mutation of the four resistance genes is from 10^{-24} to 10^{-36} . These numbers are so small that it would be impossible for us to see them (or the results of their occurrence). However, we have observed many cases of multiple resistance to antibiotics, which leaves us with the only possible conclusion that elements of bacterial genomes are

being transferred between bacteria, and producing new combinations at rapid rates. Davey and Reaney point out that plasmids have been found in all members of the enteric group of bacteria, and, indeed, have been found in practically every bacterial group which has been examined carefully for them. In addition, Davey and Reaney present a "genetic network" which illustrates the already known phage and plasmid transfer routes between genera of bacteria. In this they include two genera of the rhizoplane, eleven in the rhizosphere, three in the bulk soil, nine in "soil feces", and one of the gastrointestinal tract. There is some overlap in these groups (and in this count where one genus has been observed to occur in two habitats, it has been included in both), but the network is impressive, and strongly suggests that there is constant flow of genetic information among all of the important bacteria of a human-plant-soil system. Many of the plant-associated genera which have been discussed above are included in this network, and it is based on current knowledge which obviously is relatively undeveloped and which therefore illuminates only a small part of the interaction which must be going on.

Lacy and Leary (1979) have examined the genetic systems of bacteria which are plant pathogens and find that there is a large amount of intergeneric transfer of genetic material. Such transfer clearly is important in

provision of mechanisms to recipient bacteria which will permit them to overcome the defenses of plants. According to Lacy and Leary only the very interesting example of Agrobacterium and plant crown gall, and three species of Erwinia have been so far examined for exchange of "pathogenic" genes via plasmids. They present a table which illustrates that for many genes, there is ready plasmid transfer into a number of species of Erwinia and Pseudomonas. A large number of the plasmids to which this table (and the transfers) refer are originally from Escherichia coli (or came via E. coli), which suggests (as did Davey and Reanney) that there is widespread mixing of genetic elements among the many species making up a variety of bacterial communities.

One recent research paper (Krishnapillai and Postgate, 1980), for example, emphasizes this point when it describes the movement of his and nif genes which were derived from Klebsiella pneumoniae by plasmid into E. coli, Serratia marcescens, Erwinia herbicola, and Proteus mirabilis. Note that this short list includes bacteria usually found in several different habitats, including on (and possibly affecting) plants.

The process by which Agrobacterium tumefaciens "causes" crown gall is most interesting. The plant responds to infection by (the correct strain of) A. tumefaciens by producing a "cancerous" like growth of some of its tissues (galls). It will continue to grow more

gall tissue even after the bacterium which invaded it earlier has been killed by appropriate application of antibiotics. The reason for this is that the A. tumefaciens, after it invades the tissues of the plant, loses some of its plasmids which enter into some of the plant's cells and turns them into relatively undifferentiated, constantly growing and dividing cells. This, then, is an example of how a bacteria-carried plasmid can enter into eucaryotic cells and have major effects on their activities. How common this general kind of thing is (and the converse, where bacteria get parts of eucaryotic genomes via plasmids) is completely unknown.

There is a large amount of current literature being produced concerning plasmid carried resistance (sometimes called R-factors), especially as it applies to human disease. A couple of recent papers which give some of the flavor of this literature will be outlined. Petrocheilou, Richmond, and Bennett (1979) observed an instance in which an E. coli population bearing a resistance plasmid to tetracycline not only persisted in a woman during a period over which she was treated with ampicillin instead of tetracycline, but this E. coli also could frequently be isolated from the woman's husband. A number of studies have been made which show that babies more frequently harbor R-plasmid bearing bacteria than do healthy adults (when none of them are being given antibiotics), see Moorhouse (1969), Guinee, Ugneto, and van Leeuwen (1970),

and Eylan and Cohen (1979). This suggests that the bacteria bearing the R-plasmids may frequently be somewhat inferior competitors to individuals of the same species which do not have the plasmids in them. Guinee, Ugneto, and van Leeuwen further observed that the "normal" biota of vegetarians showed higher incidence of plasmid carried R factors than did adults who ate a more usual variety of food.

Observation of the relatively rapid rate of the evolution of bacterial populations, which are usually asexual in their reproduction, occupied the attention of several scientists well before the immensely important contribution of plasmids and phage to this evolutionary rate were realized. One kind of approach is typified by the paper of Harrison and Lawrence (1963) in which they report on the results of starvation of bacterial suspensions on the rate at which mutants were produced. In starved Aerobacter aerogenes cultures they found that there was an increase in the proportion of individuals which had a genetically based resistance to the effects of starvation. These mutants could not compete with the wild populations when nutrient was adequate, as they had a slower growth rate, but when food resources were severely limiting, they survived much better. Harrison and Lawrence concluded that these strains had an advantage, not only under conditions of severe nutrient limitation, but very possibly also when the environment fluctuated

between high and low food levels.

Maynard Smith (1968, 1974) in theoretical considerations of the effects of bacteria being haploid and asexual on their evolutionary rates, concluded that if the population was large enough, it really did not matter that the bacteria had no (or little) recombination through sex. This is because a large enough population will produce all combinations of mutations anyway, and in addition, the advantages which sexual reproduction has over the asexual form were largely determined by other assumptions which theoreticians had made. To give an idea of the size of some microbial populations (in addition to the estimates of Savage which were given above), Person, Groth, and Mylyk (1976) calculated that the mildew population on barley may be large enough to produce about 10^9 lesions/ha, each lesion produces about 10^4 conidia per day, and there are about 3.5×10^6 ha in the US. This means that about 3.5×10^{19} conidia per day are produced. Even if mutation rate of the fungus were about 10^{-5} to 10^{-6} , and this means that double mutants would occur at 10^{-10} to 10^{-12} , there nevertheless will be a large population of them (10^7 to 10^9). It is clear, however, that the production of triple mutants in this system would be much smaller, and that to produce quadruple mutants (as those discussed with respect to plasmid transport) would take a very long time. Of course, it has to be added that there are asexual populations of microorganisms which have

many orders of magnitude higher population sizes than that of the mildew just considered, and that both sexual processes and extrachromosomal mechanisms of producing recombinants are not rare.

There clearly is a mutual evolutionary adjustment between a pathogen and its host. Harlan (1976) discusses the development of what he calls a natural balance between the pathogen and the host such that little damage is done to the host. Person and Mayo (1974) also discuss this topic, and point out that at the detailed genetic level there is specific interaction which occurs between a resistance gene of the host and an avirulence gene of the pathogen.

Harlan also points out that some plant diseases require that there be some minimum density and population size of the host. This also applies to humans, for example, there are a number of diseases which have epidemic kinds of patterns. It is only after there has not been a flu or measles epidemic recently enough that there are enough susceptible individuals in the population to support an epidemic. Harlan suggests, as other examples, that diseases such as typhoid and cholera would not generally be supportable by paleolithic human populations because sub-populations were sufficiently small, compact, and isolated from each other. Similar considerations have been given to the microbial flora of people during space flight. The original idea (according

to Taylor, 1974) was that there would be considerable simplification of the microbiota during flight. This did not occur in any appreciable amount. There did tend to be some rather common changes in the abundance of the yeast Candida albicans, which could be a problem as it is a potential human pathogen. Tashpulatov and Guseva (1979) found a reduction of counts of both anaerobes and aerobes during a 16 day mission on Salyut-3, and a probably related reduction in the natural resistance of the crew.

Although it has been somewhat difficult to demonstrate as fully as one might wish, it appears that these are probably a result of the in-flight reduction of some of the microbial populations which normally are competitors of the usual human bacterial flora and of C. albicans. It should be pointed out that all flights so far experienced are relatively short, and on longer flights one would expect some extinction of species (following, in at least some respects the pattern suggested by MacArthur and Wilson, 1967).

Summary and Conclusions

1. Beyond the point that (re)supply becomes too great a problem on extra-terrestrial stations, there will be need of an agricultural system to provide for oxygen production (cycling) and food for the use of the people. This will involve primarily plants which are in current use in some of the earth's agricultural systems; chemical and single cell food production will fulfill at most only a relatively small (but perhaps important) proportion of the total required food (and vitamin) production.

2. It will probably be possible to exclude most known aggressive plant parasites and pathogens (and certainly possible to exclude plant-attacking insects, nematodes, etc.) which attack agricultural plants on earth.

3. The exclusion of human-carried microorganisms will, however be impossible (short of raising people in germ-free environments from the time they are removed aseptically from their mothers by Cesarean section).

4. Exclusion of all microorganisms may be, in any event, undesirable for several very different kinds of reasons: a) Some vitamins which humans cannot manufacture and which are unavailable in sufficient quantities in normal diets are made "for us" by bacteria in our gut (vitamin K is an example). b) It may turn out that use of microorganisms will provide the best mechanisms for the

cycling of some of the nutrients that the plants (and humans) require. c) Microorganisms may have other benefits and may prove superior to other alternatives with respect to providing them.

5. Plants produce and release into their immediate environment substantial quantities of organic materials. This includes both finely divided solid material (root cap cells, root hairs, finely divided roots, insoluble carbohydrates, and so on), and soluble organic materials. These are normally quickly used by the microbial communities of leaf surfaces and of root zones of the plants. In the absence of more or less normal microbial communities on or near surfaces of roots and leaves, these organic materials will accumulate. These concentrations of highly nutritious materials will then be invaded by some of the human carried microbial species, and we do not know what the effects on plants of some of the resulting (relatively large) populations of these microbes will be.

6. Plant pathogens which are called "aggressive" are those which can successfully attack their host species in spite of the plant's defense mechanisms; it is these which can be mostly excluded (and for which on earth the plant's normal microbial flora makes relatively little difference with respect to probability of successful attack). These pathogens commonly attack healthy, vigorous plants most effectively. Non-aggressive pathogens, on the other hand, most commonly attack when

the plant has been weakened by some kind of stress. Normal plant defense mechanisms, when the plant is healthy, vigorous, and accompanied by its normal associated microbial community, generally are adequate to defend the plant against these non-aggressive pathogens. However, evidence suggests that these and other generally non-pathogenic microbial species will be successful in attack on plants in the absence of appropriate (the normal) microbial communities of leaf, shoot, and root zones.

7. The ecological roles vis-a-vis the plants which are normal to the non-pathogenic microbiota of the plant's root zone include: a) Competition with the plant for nutrients especially in the presence of high levels of available carbohydrate (these problems, however, can easily be avoided by adequate system design and management), b) Competition with other species of microorganisms, including pathogens, for plant produced particulate and dissolved nutrients, (frequently to the point that the pathogens cannot survive--in some saprophytic microbial species this competitive success is effected through the production of antibiotics), c) Augmentation, transportation, and/or mobilization of nutrients for/to the plant, d) Production of plant growth affecting compounds (the effects of stimulating substances is one reason that plants which are accompanied by their normal microbial communities are larger than otherwise

similarly treated but germfree plants), e) Manufacture of plant nutrients (for example, provision of available nitrogen by nitrogen fixation), f) "Permanent" removal of plant nutrients from the system (denitrification, for example), and, g) No doubt other activities.

Many of the plant associated microbes are beneficial, and sometimes of considerable importance to the wellbeing and yield of "their" plants. It appears likely that even if the vital protective functions of the normal microbiota (or of subcommunities derived from it) are not considered, the other benefits of the presence of microorganisms would be great enough to more than offset the costs of choice, inclusion and manipulation of appropriate assemblages of them in extra-terrestrial, self sufficient stations. This is because microbiological systems have major advantages of small size, greatly diverse abilities, and repair and reproductive capacities.

8. A possible scenario of a major kind of problem which might develop in extra-terrestrial stations which have had the addition of originally axenic plants, is that plant exudates and the cells, root hairs, and other parts of the plant which die normally, will sooner or later produce rich media on which bacterial and fungal populations will grow. As these pools of good microbial food develop there will be an increasing probability that some of the human-carried microbiota will invade them. Experiments need to be carried out to determine if some of

these human derived populations (under these very unnatural conditions) will attack or otherwise harm the plants, and if so (as seems probable), to learn what ameliorative methods may be used.

9. Also, there are possibilities that other than the unavoidable human-carried pool of microorganisms might be involved in the kinds of attacks suggested above. It may be that additional microbial species would be highly desirable within the system where they would carry out specific needed processes and that some of these species could cause problems for the plants (especially if the plants originally were axenic). For example, bacteria and fungi (in high temperature reactors?) may best provide for sewage treatment and for the destruction of other microbial, plant or human produced organic materials. Other microbial systems may be required for the most space and weight efficient elimination of volatiles which will be produced in the system (hydrogen, methane and ethylene, for example). Biological processes also probably will provide the most efficient mechanism for nitrogen fixation in a system most likely containing ongoing denitrification activity. Also, microorganisms could provide some of the nutrients required in the human diet but which might not be (sufficiently) produced by the (relatively simple) agricultural system. Vitamin B-12 producers (yeast, for example) will be needed if animals are not used for food. If food animals are taken (goats, rabbits, termites?),

they may have microbial requirements. Microbes also could provide for the production of beer and wine (and for cheese and yogurt if goats or other milk animals are taken). Microorganisms also might be useful in providing for other needs of the system.

10. We cannot avoid taking some microorganisms with us. It is my estimate that we will also intentionally include a number of microbial species on long term human supporting extraterrestrial stations because of their efficient function as versatile factories which have small space and weight requirements and which are self repairing. Because of these microbes (especially the unavoidable ones), I believe that we also will need to include more or less normal, although carefully screened and constructed, microbial communities. These will live on and near the surfaces of our agricultural plants and protect them from deleterious effects of the other microorganisms.

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16. Abstract <p>An analysis of the available literature suggests that human-carried microorganisms, which cannot practically be excluded (at this time) from human supporting agricultural systems of extra-terrestrial stations, may be an important problem. This is because these microorganisms may have several kinds of deleterious effects; some of these, especially those which might damage the plants on which the people depend for oxygen and food, could be extremely serious. It appears that this potential problem can be avoided by the inclusion of carefully screened or constructed, but more or less normal phylloplane and rhizosphere microbial communities.</p>			
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